

## Chapter 11

# New Taxa of Nesomyine Rodents (Muroidea: Muridae) from Madagascar's Northern Highlands, with Taxonomic Comments on Previously Described Forms

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### Abstract

Field survey of the Réserve Spéciale d'Anjanaharibe-Sud has disclosed previously unknown taxa of Nesomyinae from Madagascar's northern highlands, a vast region heretofore poorly documented for the island's indigenous rodents. We diagnose and compare: a new species of *Eliurus* whose morphology suggests relationship to another recently described form, *E. petteri* from east-central Madagascar; and a new genus and species of Nesomyinae with attributes that indicate closest affinity, among the eight genera currently recognized, to *Eliurus*. The new forms originate from middle montane to sclerophyllous montane forest within the reserve (1250–1950 m). Evidence for the specific status of *E. ellermani* is reviewed, and its type locality is amended. Although museum and field studies in the last decade have revised upwardly the number of Nesomyinae, doubling the number of species known, the expectation that their diversity will match that of rodents on comparably sized tropical islands seems doubtful.

### Résumé

L'inventaire mené dans la Réserve Spéciale d'Anjanaharibe-Sud a permis la découverte, au niveau des zones d'altitude du nord de Madagascar, de taxons de Nesomyinae jusqu'alors inconnus, provenant d'une vaste région pourtant fort mal connue sur le plan de la faune endémique des rongeurs. Nous avons établi une diagnose et comparé une nouvelle espèce d'*Eliurus* dont la morphologie laisse à penser qu'elle puisse avoir des relations avec *E. petteri*, une autre espèce récemment décrite du centre-est de Madagascar, et une nouvelle espèce appartenant à un nouveau genre de Nesomyinae dont certains attributs indiquent une proche affinité avec le genre *Eliurus*, un des huit genres actuellement reconnus dans la sous-famille des Nesomyinae. Cette nouvelle forme a été rencontrée au sein de la réserve, depuis la forêt de moyenne altitude jusqu'au fourré sclérophylle de montagne, soit entre 1250 et 1950 m d'altitude. L'évidence du statut particulier d'*E. ellermani* est commentée et la localité du type est complétée. Bien que des études muséologiques et de terrain aient, au cours des dix dernières années, permis d'amender considérablement le nombre d'espèces de Nesomyinae, en doublant leur nombre, l'idée que la diversité de ces espèces atteigne la diversité de rongeurs constatée dans des îles tropicales de taille similaire, semble improbable.

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## Introduction

To date, few species of Madagascar's indigenous rodents (Muridae: Nesomyinae) have been documented from the rugged northern highlands of the island. For example, the rodent denizens of montane forest and alpine habitat on the vast Tsaratanana Massif, isolated from the Central High Plateau, are virtually unknown: only two species and three specimens of Nesomyinae, one *Eliurus minor* and two *Nesomys rufus*, have been reported previously (Carleton & Schmidt, 1990; Carleton, 1994). The 1994 small mammal survey of the Réserve Spéciale (RS) d'Anjanaharibe-Sud, which straddles the eastern portion of these northern mountains, thus constitutes the first concerted attempt to address this conspicuous geographic void in understanding nesomyine diversity and distribution.

This chapter provides the systematic context and nomenclatural background for certain nesomyine forms reported in Chapter 12, which covers their populations and natural history. Our short prodromus includes the discovery of a new species of *Eliurus*, commentary on the taxonomic status of a previously named form of *Eliurus*, and diagnosis of a new genus and species of Nesomyinae.

## Materials and Methods

The material from the RS d'Anjanaharibe-Sud consists of conventional round skulls with skulls, as well as complete skeletons and fluid-preserved whole carcasses, and is housed in the Field Museum of Natural History (FMNH), Chicago, and the Département de Biologie Animale, Université d'Antananarivo (UA), Antananarivo. Specimens already deposited in the latter institution are referenced by the collector's field numbers (UA-SMG) in lieu of catalog numbers. Relevant series of Nesomyinae used in the various tabular summaries, numerical analyses, and anatomical comparisons were examined by M.D.C. from the following collections: the American Museum of Natural History (AMNH), New York City; the Natural History Museum (BMNH), London; the Museum of Comparative Zoology (MCZ), Harvard University, Cambridge; the Muséum National d'Histoire Naturelle (MNHN), Paris; and the National Museum of Natural History (USNM), Smithsonian Institution,

Washington, D.C. Museum numbers and locality data are provided in Appendix 11-1.

Six measurements, in millimeters (mm) or grams (g), were taken by S.M.G. for each FMNH specimen in the flesh; their abbreviations and definitions are given below. Dimensions from other museum specimens are those given by collectors on skin tags or in field catalogs. Dry hindfoot length was recorded by M.D.C. to the nearest 0.5 mm, especially on older museum specimens, which typically lack any external data. External measurements are tabulated for the purposes of general description and field identification but were not used in multivariate comparisons of samples.

- TOTL = total length of body and tail, measured from the tip of the nose to the end of the caudal vertebrae (not including terminal hair tuft).  
HB = head and body length, as measured in the field, from the tip of the nose to the distalmost point of the body (at base of tail).  
TL = tail length, measured from the base of the tail (held at right angle to the body) to the end of the last caudal vertebra (not including terminal hair tuft).  
HF = hindfoot length, measured from the heel to the tip of the longest toe (not including claw).  
DHF = dry hindfoot length, measured from the heel to the tip of the claw of the longest toe, on skins whose metatarsal and phalangeal bones remained straightly aligned.  
EL = ear length, measured from the basal notch to the distalmost rim of the pinna.  
WT = weight, measured in grams with Pesola spring scales to within 0.5 g for animals weighing less than 100 g and to within 1.0 g for those weighing between 101 and 300 g.

Sixteen cranial and two dental dimensions were measured by M.D.C. to the nearest 0.1 mm using handheld digital calipers accurate to 0.03 mm. These measurements, and their abbreviations, follow the anatomical landmarks defined and illustrated in Carleton (1994):

- BBC = breadth of the braincase  
BIF = breadth of incisive foramina  
BMIs = breadth of the bony palate across the first upper molars

BOC = breadth across the occipital condyles  
 BR = breadth of rostrum  
 BZP = breadth of the zygomatic plate  
 DAB = depth of the auditory bulla  
 IOB = interorbital breadth  
 LBP = length of bony palate  
 LD = length of diastema  
 LIF = length of the incisive foramina  
 LM1-3 = coronal length of maxillary tooth row  
 LR = length of rostrum  
 ONL = occipitonasal length  
 PPB = posterior breadth of the bony palate  
 PPL = postpalatal length  
 WM1 = width of the first upper molar  
 ZB = zygomatic breadth

Standard descriptive statistics and multivariate analyses were carried out using Systat (version 7.0, 1996). Morphological terms generally follow Carleton (1980) and Voss (1988); names of dental structures follow Reig (1977), as illustrated by Carleton and Musser (1989); the rationale for various character polarities discussed in the text is elaborated by Hershkovitz (1962), Bugge (1970), Carleton (1980, 1994), Voss (1988, 1993), and Carleton and Musser (1989). Field methods for the FMNH specimens originating from the RS d'Anjanaharibe-Sud are described by Goodman and Carleton in Chapter 12.

## The Tufted-Tail Rats, Genus *Eliurus*

Among the rodent collections obtained from moist forest in the RS d'Anjanaharibe-Sud are samples of five species of *Eliurus*. Three of these, *E. majori* Thomas (1895), *E. minor* (Major, 1896a), and *E. webbi* Ellerman (1949), can be confidently associated with forms already described and known from other regions of Madagascar (see Chapter 12 for registration numbers and full provenience). The three can be easily distinguished from one another on the basis of external and cranial size (Figs. 11-1-11-3, Table 11-1) in addition to other qualitative traits of the pelage and skull that define their morphologies (Carleton, 1994). The identity of two species, both with tails tipped with fine white hairs, is problematic and warrants additional commentary and comparisons to justify their specific assignment. One of these forms is described as new to the island's indigenous rodent fauna; the other raises questions about the validity of *E. ellermani* Carle-

ton (1994), a recently named species related to *E. tanala*.

## The Smaller White-tailed Species

This medium-sized *Eliurus* was relatively abundant at 1260 m, where 26 individuals were live-trapped within a period of 6 days. Only one was collected at 1550 m, but none was taken at the lowest (875 m) or highest (1950 m) sites surveyed. Specimens of the medium-sized, white-tailed *Eliurus* exhibit several features that recall *E. petteri*, a species named from humid forest in east-central Madagascar (Carleton, 1994), yet it is otherwise strongly differentiated from the latter as well, as detailed below. We name it as a new species.

### *Eliurus grandidieri*, new species

(Figs. 11-1-11-6, 11-11; Table 11-2)

**HOLOTYPE**—Field Museum of Natural History number 154048, skin and skull of young adult female (original number SMG 7066), collected 20 November 1994 by Steven M. Goodman.

Standard measurements (in mm) from the skin tag of the type include the following: TOTL, 324; HB, 132; TL, 186; HF (without claw), 27 (DHF, as measured by M.D.C. with claw, 28); EL, 21; and WT (in g), 59.5. The female carried two embryos (crown-rump length, 10 mm), one each in the left and right uterine horns. The habitat is noted on the specimen tag as "In upper montane forest. Trap on ground at opening of large hole under root clump and covered with debris."

The condition of the skin is good, although its right side is somewhat tucked due to uneven drying of the specimen (Fig. 11-4). The condition of the skull is excellent, its cranial and mandibular processes wholly intact (Fig. 11-5).

**TYPE LOCALITY**—Madagascar, Province d'Antsiranana, Réserve Spéciale d'Anjanaharibe-Sud, 11 km WSW of Befingitra, 1550 m, 14°44.5'S, 49°27.5'E (as given by the collector).

**DIAGNOSIS**—A species of *Eliurus* characterized by medium size (HB  $\approx$  125–135 mm, HF  $\approx$  27–29 mm, ONL  $\approx$  34–35.5 mm), in general larger than *E. minor* and smaller than *E. petteri* or *E. webbi*. Dorsal pelage finely textured and dark, underparts dark gray (bright white in *E. petteri*); tail having weakly developed terminal tuft of white hairs (dark to tip in *E. petteri*), caudal vertebrae

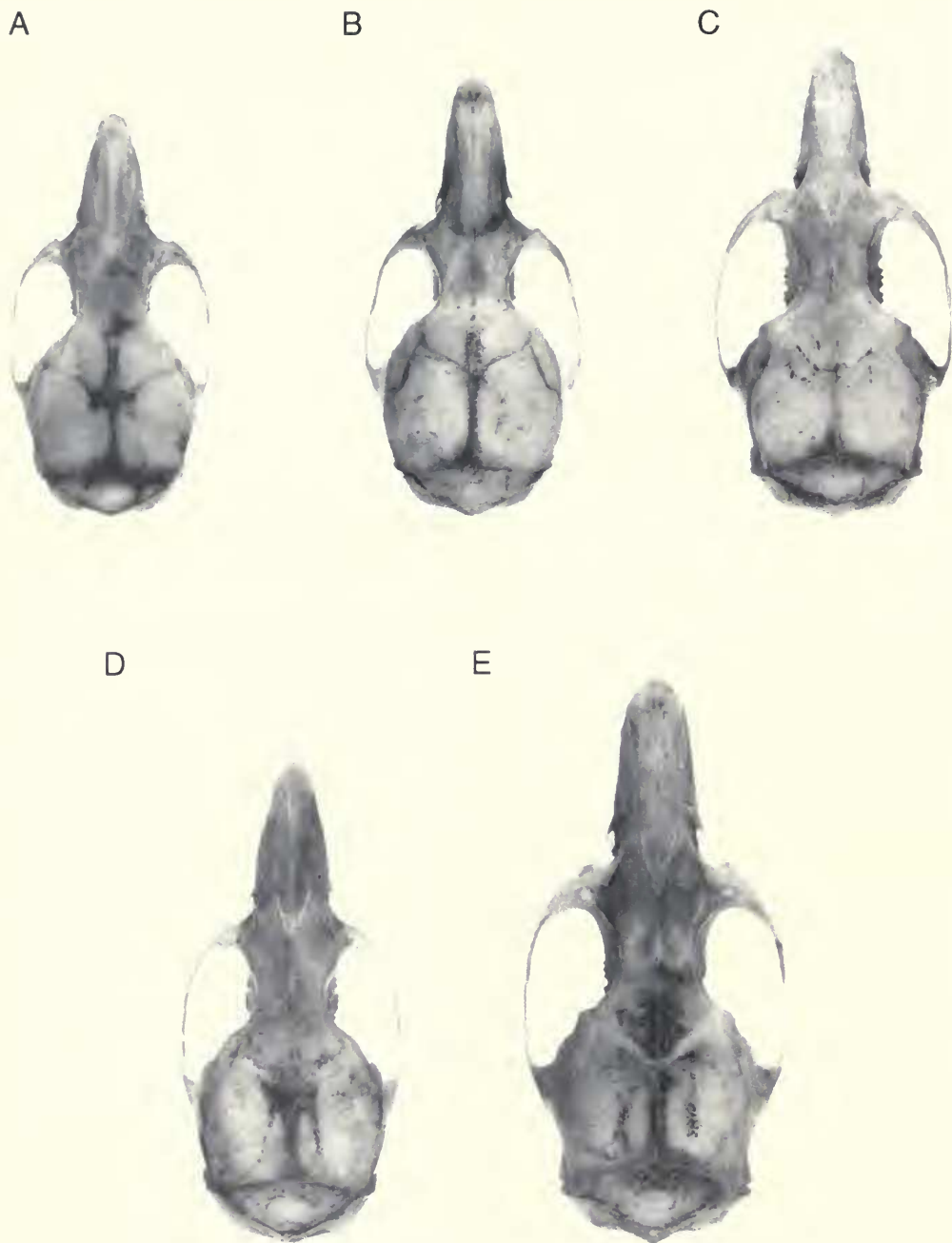


FIG. 11-1. Dorsal view ( $\times 1.75$ ) of adult crania of the five species of *Eliurus* that occur in the RS d'Anjanaharibe-Sud. A, *E. minor* (FMNH 154042: male, ONL = 32.0 mm). B, *E. grandidieri*, new species (FMNH 154048: female, holotype, ONL = 35.3 mm). C, *E. majori*. (FMNH 154054: female, ONL = 37.8 mm). D, *E. webbi* (FMNH 154251: male, ONL = 38.2 mm). E, *E. tanala* (FMNH 154250: female, ONL = 45.7 mm).

relatively long (TL 127% of HB) for the genus (TL 115–120% of HB in most species); and narrow dusky streak extending over middle of metatarsus. Cranium possessing moderately expansive

zygomatic arches (bowed little in *E. petteri*), tiny ectotympanic bullae, and moderately long and wide incisive foramina (very short and narrow in *E. petteri*); mandible lacking capsular process, in-



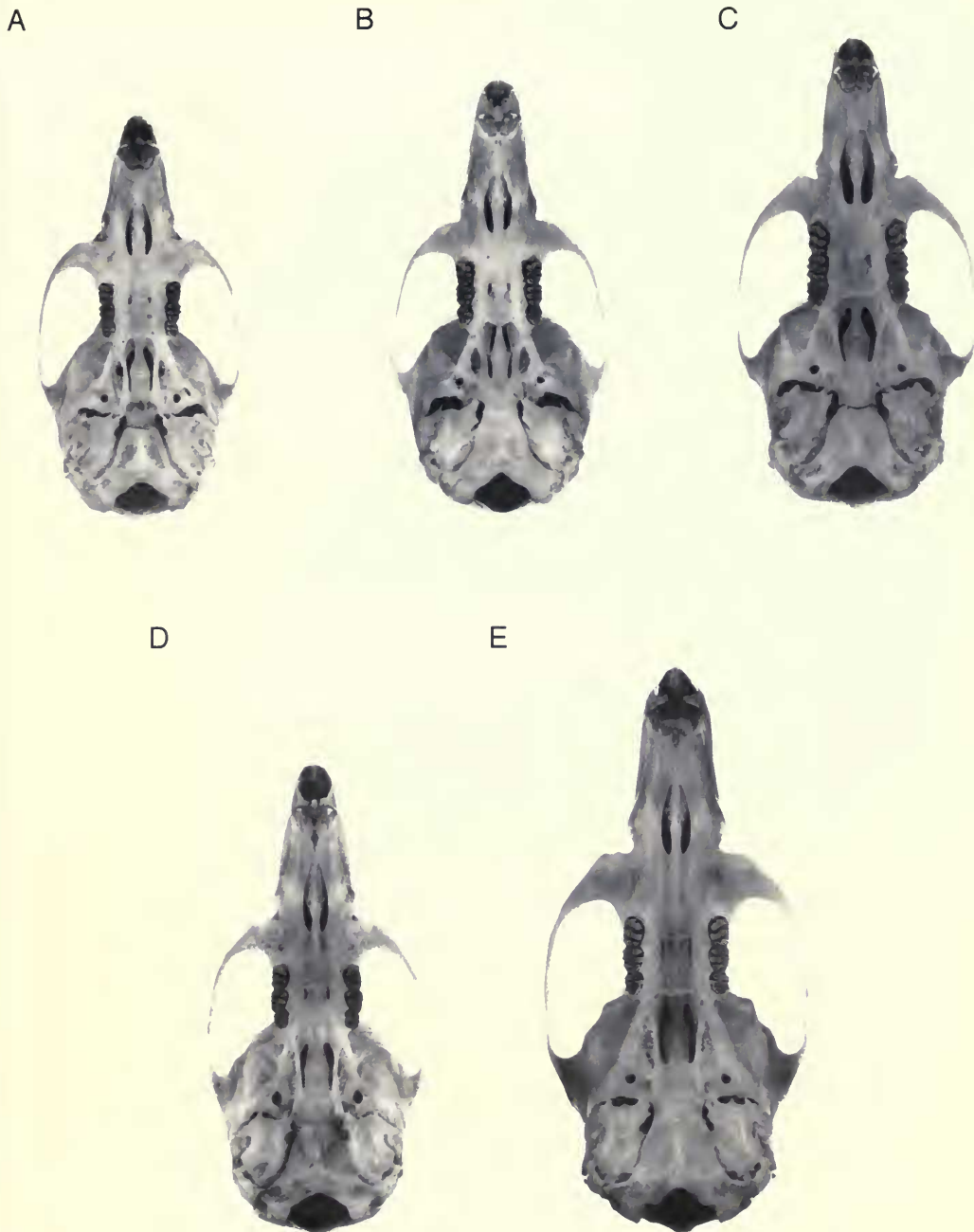


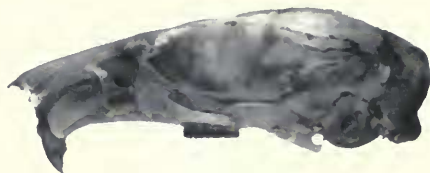
FIG. 11-2. Ventral view ( $\times 1.75$ ) of adult crania of the five species of *Eliurus* that occur in the RS d'Anjanaharibe-Sud. A, *E. minor*. B, *E. grandidieri*, new species. C, *E. majori*. D, *E. webbi*. E, *E. tanala*. Same specimens as illustrated in Figure 11-1.

cisor alveolus extremely short; upper and lower incisors among the narrowest in the genus (only matched by *E. petteri*), but molar rows somewhat long and robust.

REFERRED SPECIMENS—Province d'Antsiranana,

RS d'Anjanaharibe-Sud, 9.2 km WSW of Befingitra, 1260 m,  $14^{\circ}44.7'S$ ,  $49^{\circ}27.7'E$  (FMNH 154046, 154047, 154253–154257, 154259–154265, 154288, 154290–154292; UA-SMG 6913, 6936, 6937, 6944–6946, 7002, 7006). All referred specimens were also

A



B



C



D



E



FIG. 11-3. Lateral view ( $\times 1.75$ ) of adult crania of the five species of *Eliurus* that occur in the RS d'Anjanaharibe-Sud. A, *E. minor*. B, *E. grandidieri*, new species. C, *E. majori*. D, *E. webbi*. E, *E. tanala*. Same specimens as illustrated in Figures 11-1 and 11-2.

TABLE 11-1. Comparison of selected external and craniodental measurements of *Eliurus minor*, *E. webbi*, and *E. majori*, the three dark-tailed species from the RS d'Anjanaharibe-Sud.\*

Variable	<i>E. minor</i> <sup>†</sup>	<i>E. webbi</i> <sup>‡</sup>	<i>E. majori</i> <sup>§</sup>
TOTL	244.0 ± 16.9 205.0–260.0	309.7 ± 14.4 294.0–332.0	354.4 ± 11.4 330.0–370.0
HB	110.4 ± 4.4 105.0–116.0	142.0 ± 4.8 138.0–149.0	158.6 ± 3.4 155.0–165.0
TL	127.7 ± 14.6 94.0–139.0	163.5 ± 10.1 153.0–179.0	186.6 ± 8.9 170.0–202.0
HF	22.1 ± 0.8 21.0–23.0	27.7 ± 1.5 26.0–29.0	29.3 ± 1.1 27.0–31.0
WT	36.9 ± 4.1 31.0–43.5	71.9 ± 5.9 63.5–78.5	94.2 ± 10.5 78.0–109.0
ONL	32.0, 32.3	38.2 ± 0.7 37.2–39.1	38.4 ± 1.0 36.5–39.8
ZB	15.8, 15.9	17.9 ± 0.6 17.1–18.8	19.1 ± 0.7 18.3–20.6
BBC	12.2, 12.3	14.0 ± 0.3 13.6–14.3	14.2 ± 0.3 13.8–14.8
IOB	5.1, 5.4	5.7 ± 0.2 5.3–5.9	5.3 ± 0.1 5.2–5.5
LR	10.6, 10.9	13.4 ± 0.5 12.5–14.0	13.3 ± 0.7 12.1–14.3
BR	5.5, 6.0	7.0 ± 0.5 6.6–7.9	7.1 ± 0.3 6.6–7.6
PPL	11.2, 11.3	13.6 ± 0.7 13.0–14.9	13.6 ± 0.5 12.7–14.4
LBP	6.6, 6.9	8.0 ± 0.4 7.3–8.3	7.6 ± 0.4 7.1–8.1
LIF	4.0, 4.6	5.5 ± 0.2 5.3–5.8	6.2 ± 0.4 5.7–6.9
BIF	2.0, 2.1	2.1 ± 0.1 2.0–2.4	2.6 ± 0.1 2.4–2.9
LD	9.1, 9.3	11.1 ± 0.3 10.8–11.6	10.9 ± 0.5 10.2–11.6
BM1s	5.9, 6.5	7.4 ± 0.2 7.1–7.6	7.9 ± 0.2 7.5–8.3
DAB	4.7, 4.9	5.1 ± 0.1 5.0–5.2	5.3 ± 0.3 5.2–6.0
BZP	2.6, 2.9	3.2 ± 0.1 3.0–3.4	3.3 ± 0.2 3.0–3.6
BOC	6.8, 7.3	8.3 ± 0.2 7.9–8.6	8.5 ± 0.4 7.9–8.9
LM1-3	4.29, 4.39	5.10 ± 0.15 4.90–5.31	6.62 ± 0.12 6.40–6.78
WM1	1.20, 1.25	1.44 ± 0.07 1.34–1.54	1.73 ± 0.08 1.60–1.81

\* Sample statistics include the mean ± 1 SD and the observed range.  
† For external variables, N = 8 (FMNH 154042, 154043, and 154246–154248; UA-SMG 6880, 6974, and 6980); for cranial variables, N = 2 (FMNH 154042 and 154043).  
‡ For external and cranial variables, N = 6 (FMNH 154035–154038, 154251, and 154252).  
§ For external variables, N = 11 (FMNH 154052–154054, 154242–154245, and 154289; UA-SMG 6981, 6998, and 7090); for cranial variables, N = 9 (FMNH 154052–154054, 154242–154245, 154266, and 154289).

collected by S.M.G. between 4 and 9 November 1994 as part of the same inventory and variously prepared as skin with skull, complete skeleton, fluid-preserved carcass with skull removed, or whole carcass in fluid.

DISTRIBUTION—At present known only from

moist montane forest between 1260 and 1550 m in the RS d'Anjanaharibe-Sud. The species may be expected in other highlands of northern Madagascar, e.g., the Tsaratanana massif.

MORPHOLOGICAL DESCRIPTION—Caudal pilosity weakly expressed (tuft much less developed com-



FIG. 11-4. Dorsal and ventral aspects of the skins of *Eliurus grandidieri*, new species (FMNH 154048: holotype; Antsiranana Province, RS d'Anjanaharibe-Sud) (**left pair**), and *E. petteri* (USNM 341825: paratype; Toamasina Province, 18 km E of Périnet) (**right pair**).





FIG. 11-5. Dorsal, ventral, and lateral views of the cranium and lateral view of the mandible of the holotype (FMNH 154048; ONL = 35.3 mm) of *Eliurus grandidieri*, new species.

pared with the smaller *Eliurus minor*), with noticeable penicillate section limited to distal 25–30% of tail length and the hairs short, 7–8 mm. Tail tipped with fine white hairs, this terminal white tuft varying from 15 to 35 mm long (Fig. 11-11). Caudal epidermis unpigmented over terminal segment, coincident with extent of white tuft; proximal 70–75% of tail length pigmented dark gray dorsally, irregularly mottled with white splotches ventrally (i.e., not sharply or evenly bicolored). Proximal scutellation moderately coarse, about like *E. minor* but heavier than *E. petteri*; basal scale hairs short (about one annulation long) and inconspicuous, tail appearing naked over proximal half.

Dorsal pelage relatively short and close set (8–9 mm on midrump), texture fine and soft, conveying a sleek appearance. Cover hairs of dorsum tricolored, long basal segment of plumbeous gray, short middle band of warm buff, and very short tip of dark brown to blackish; guard hairs dark brown but inconspicuous, extending only slightly above cover fur. General effect of upperparts a sooty brown to charcoal gray, denser concentration of black toward mediodorsum and browner on flanks, overall tone somber. Narrow dusky streak over tarsus and metatarsus usually well defined; remainder of metatarsus and phalanges, including ungual tufts over claws, clothed with clear white hairs; tops of forefeet white, dark dorsal pelage ending at carpus. Ventral cover hairs bicolored, basal two-thirds plumbeous gray, and distal third dull to clear white; general impression of underparts a medium to dark gray, distinct from but not sharply contrasted with muted dorsum. Longest mystacial vibrissae about 40–50 mm, extending behind pinnae when appressed to skin; genal vibrissae extremely short (absent?). Pinnae dark, appearing naked to unaided eye, but invested externally with short brown hairs and internally with fine white ones.

Skull moderate in size and construction, intermediate to *Eliurus minor* and *E. webbi* in general aspect but with a proportionally longer rostrum (Figs. 11-1–11-3; Tables 11-1, 11-2). Configuration of interorbital region, braincase, and zygomatic plate as per the genus (Carleton, 1994). Zygomatic arches moderately stout for size of skull, deeper over midsection than delicate arches of *E. petteri*; lateral bowing more pronounced toward rear of zygoma, at squamosal–jugal contact, and converging toward zygomatic plates. Incisive foramina typical for the genus, about 46% of diastemal length, longer and wider than those of *E. petteri* (LIF about 38% of LD). Posterior palatal foramina formed as a single pair of small oval openings, no development of supernumerary palatal perforations or elongate slits as in some *Eliurus* (such as *E. minor* and *E. tanala*). Anterior margin of mesopterygoid fossa broadly horseshoe-shaped, extending slightly between third molars, about one-third their length. Subsquamosal fenestra and postglenoid foramen open fully in all specimens, revealing lumen of braincase, hamular process neatly delineated. Alisphenoid strut present on holotype, but of 12 specimens with cleaned skulls, four without any evidence of this bony partition between the buccinator–masticatory and accessory oval forami-

TABLE 11-2. Comparison of selected external and craniodental measurements of *Eliurus grandidieri*, new species, and *E. petteri* Carleton (1994).\*

Variable	<i>E. grandidieri</i> (Holotype) <sup>†</sup>	<i>E. petteri</i> (Holotype) <sup>‡</sup>	<i>E. grandidieri</i> (Type Series) <sup>§</sup>	<i>E. petteri</i> (Type Series) <sup>  </sup>
TOTL	324.0		293.4 ± 13.4 275.0–324.0	314.0
HB	132.0	130.0	127.3 ± 4.4 118.0–135.0	133.0 130.0, 136.0
TL	186.0	185.0	161.7 ± 12.3 141.0–186.0	181.5 178.0, 185.0
HF	28.5	33.0	27.7 ± 0.8 26.0–29.0	33.5 33.0, 34.0
WT	59.5		52.8 ± 5.5 44.5–67.5	74.0
ONL	35.3	38.4	34.7 ± 0.6 33.5–35.6	38.3 ± 0.6 37.6–38.8
ZB	17.6	17.9	16.8 ± 0.9 15.0–17.8	17.2 ± 0.7 16.6–17.9
BBC	13.5	13.8	13.1 ± 0.5 12.4–14.0	13.4 ± 0.3 13.1–13.8
IOB	5.5	5.2	5.4 ± 0.1 5.2–5.6	5.4 ± 0.2 5.2–5.6
LR	12.9	13.9	12.4 ± 0.3 11.9–12.9	13.5 ± 0.5 13.0–13.9
BR	6.4	6.7	6.3 ± 0.3 5.9–7.0	6.6 ± 0.1 6.5–6.7
PPL	11.9	13.4	11.7 ± 0.4 10.8–12.2	13.5 ± 0.4 13.1–13.9
LBP	7.7	8.4	7.3 ± 0.3 6.7–7.7	8.1 ± 0.5 7.6–8.4
LIF	4.4	4.1	4.7 ± 0.3 4.3–5.0	4.0 ± 0.2 3.7–4.1
BIF	2.2	2.1	2.2 ± 0.2 2.0–2.7	2.0 ± 0.1 1.9–2.1
LD	10.0	10.9	10.1 ± 0.3 9.3–10.4	10.6 ± 0.3 10.4–10.9
BM1s	6.8	6.9	6.9 ± 0.2 6.5–7.2	6.9 ± 0.3 6.6–7.1
DAB	5.0	5.2	4.5 ± 0.2 4.1–5.0	5.0 ± 0.2 4.8–5.2
BZP	3.0	3.3	3.1 ± 0.2 2.7–3.4	3.2 ± 0.1 3.1–3.3
BOC	7.9	8.3	7.8 ± 0.2 7.3–8.0	8.2 ± 0.1 8.0–8.3
LM1-3	5.38	5.05	5.42 ± 0.11 5.29–5.63	5.01 ± 0.1 4.90–5.09
WM1	1.56	1.38	1.52 ± 0.05 1.43–1.61	1.40 ± 0.06 1.35–1.47

\* Sample statistics include the mean ± 1 SD and the observed range.

<sup>†</sup> FMNH 154048.

<sup>‡</sup> MNHN 1961.177

<sup>§</sup> For external variables, N = 19–23 (FMNH 154046–154048, 154253, 154254, 154256, 154257, 154259, 154260, 154262–154264, 154288, 154290, and 154291; UA-SMG 6913, 6936, 6937, 6944–6946, 7002, and 7006); for cranial variables, N = 12 (FMNH 154046–154048, 154257, 154262, 154265, 154288, and 154290–154292; UA-SMG 6936 and 6945).

<sup>||</sup> For external variables, N = 1 or 2 (MNHN 1961.177; USNM 341825); for cranial variables, N = 3 (MCZ 45928; MNHN 1961.177; USNM 341825).

na. Ectotympanic bullae tiny, relatively as small as those of *E. petteri*, wide posteroventral expanse of periotic correspondingly visible.

Upper and lower incisors delicate, thin in width and depth like those of *Eliurus petteri*; enamel face of incisors yellow to very pale orange. Upper incisors more nearly orthodont; alveolus of lower incisor short, terminating at the level of the coronoid process and low on the ascending ramus, without lateral protuberance as a capsular process. Upper and lower third molars shorter than second molars as in most *Eliurus*, unlike relatively large third molars of *E. majori* and *E. penicillatus*.

NOTES ON NATURAL HISTORY—Individuals of *Eliurus grandidieri* occurred sympatrically with those of *E. majori*, *E. minor*, *E. tanala* (see following account), *Gymnuromys roberti*, and *Nesomys rufus*, as well as the ubiquitous commensal *Rattus rattus*. Several of these nesomyines are themselves restricted to middle or upper montane zones (*E. majori*, *E. tanala*, and *N. rufus*) or are widely ranging in altitudinal occurrence (*E. minor* and *G. roberti*).

ETYMOLOGY—The species epithet, *grandidieri*, recognizes the early contributions of the explorer and naturalist Alfred Grandidier to understanding Madagascar's unique biota and insular geography. The elder Grandidier was among the first to appreciate the uniqueness of the fauna, including its rodents. He discovered the first examples of and later described the giant rat *Hypogeomys antimenae* (Grandidier, 1869) and collected the first specimen of a tufted-tail rat, later described by Milne Edwards (1885) as the type species, *myoxinus*, of his new genus *Eliurus*.

TAXONOMIC COMPARISONS—Grandidier's tufted-tailed rat is an attractive and distinctive species. At first glance, its external appearance suggests a gracile version of *Eliurus tanala*, and its skull resembles an oversized example of *E. minor* with a longer rostrum. In external and cranial dimensions, *E. grandidieri* surpasses examples of *E. minor* but is notably smaller than those of *E. webbi* and *E. majori* (compare Tables 11-1 and 11-2). Its terminal caudal plume of white hairs offers clear-cut visual separation from examples of the latter three species, all of which have completely dark-furred tails. The robust size of the second species with a white-tipped tail, whose taxonomic assignment is discussed next, permits no confusion with the much smaller *E. grandidieri*. In addition to size and a long tail with a terminal white tuft, the short alveolus

of the lower incisor and the absence of a capsular process segregate *E. grandidieri* from other species of *Eliurus* found in the reserve (Figs. 11-6, 11-11). Extended comparison and contrast are required to only one other species, *E. petteri*, a form known by just three specimens from three nearby localities in the vicinity of RS d'Analamazaotra, east-central Madagascar (Carleton, 1994).

*Eliurus grandidieri* and *E. petteri* share certain anatomical traits that are uncommon among described forms of *Eliurus* and that implicate each as the other's closest relative within the genus. The dorsal pelage of both appears sleek and relatively short, its texture fine and soft; the color is dark and the tone muted. The dark color of the upperparts extends onto the metatarsi of both species as a median dusky streak. The two have a weakly developed terminal caudal tuft, the hairs short and the notably penicillate expansion confined to the distal one-quarter of tail length (distal one-third or more in other *Eliurus*); the contrast is well conveyed by comparison to the dense, long caudal tuft characteristic of the smaller-bodied *E. minor*. In spite of the undistinguished terminal tuft, the tails of *E. grandidieri* and *E. petteri* are relatively the longest in the genus, about 125–135% of head and body length compared with 115–120% in most *Eliurus*. Other proportional similarities include their uninflated ectotympanic bullae, which are relatively the smallest within the genus (the absolute depth of the bulla is approximately equal to that of the smaller *E. minor*; Tables 11-2, 11-7), and the exceptionally delicate construction of their upper and lower incisors, again qualifying as extreme in this regard for the genus. The three known individuals of *E. petteri* and a minority of *E. grandidieri* specimens (four of 12 skulls) lack an alisphenoid strut, a feature whose absence is interpreted as derived; the strut is uniformly present on all specimens of other *Eliurus* species so far examined (Carleton, 1994). Lastly, the lower incisor of both species lacks any lateral protrusion as a capsular process and is unusually short, ending at the level of the coronoid process and low on the ascending ramus (Fig. 11-6). In other *Eliurus*, the alveolus of the lower incisor terminates as a discernable lateral bulge set more dorsal and rearward on the ascending ramus.

Although such singular resemblances of *Eliurus grandidieri* and *E. petteri* offer preliminary support for their close kinship, as many differences highlight their status as separate species.

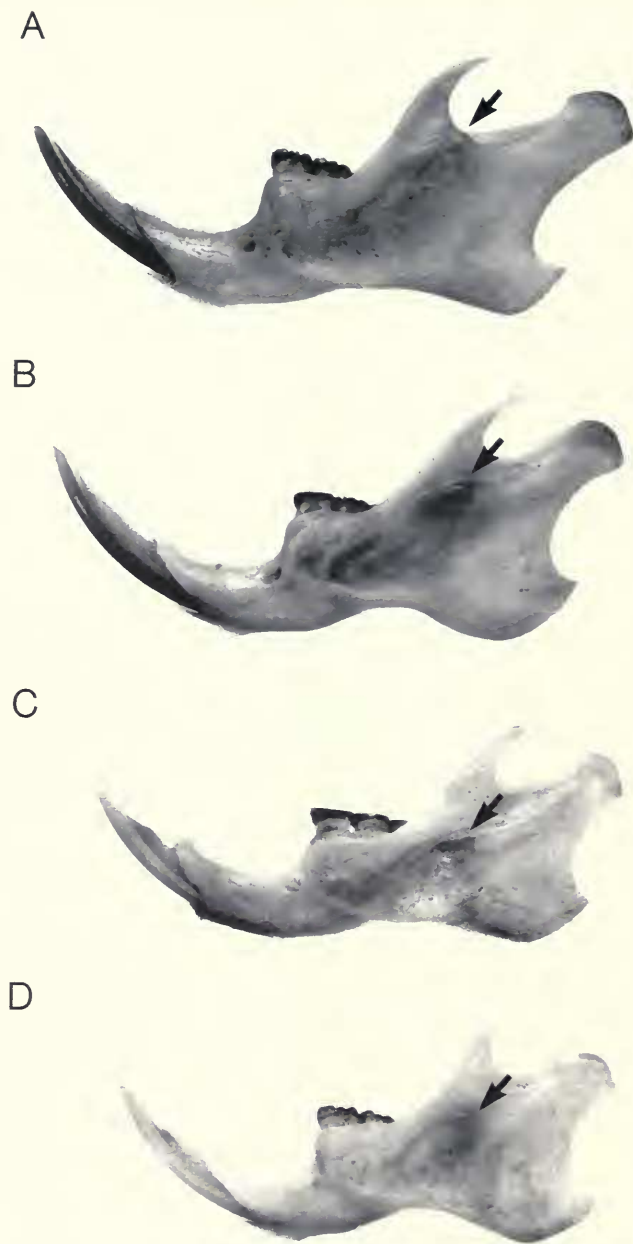


FIG. 11-6. Lateral view ( $\times 3$ ) of left mandibles of four species of *Eliurus*. **A**, *E. tanala* (USNM 448983: Ambodiamontana). **B**, *E. webbi* (USNM 448993: 0.5 km N of Kianjavato). **C**, *E. petteri* (USNM 341825: 18 km E of Périnet). **D**, *E. grandidieri*, new species (FMNH 154048: RS d'Anjanaharibe-Sud). Arrows point to the dorsalmost and posteriormost extension of the incisor alveolus.

Two chromatic traits of the skin provide externally obvious means of discrimination: the definition of the tail tuft, white-tipped in *E. grandidieri* versus brownish gray in *E. petteri* (Fig. 11-11), and the dorsal-ventral pelage contrast, gray venter in *E. grandidieri* versus bright white un-

derparts in *E. petteri* (Fig. 11-4). *E. petteri* is the bigger of the two species, as judged by most measurements of the skin and skull (Table 11-2). Although larger in most extremal dimensions, the thin zygoma and longer, narrow rostrum of *E. petteri* convey a more gracile cranial construc-



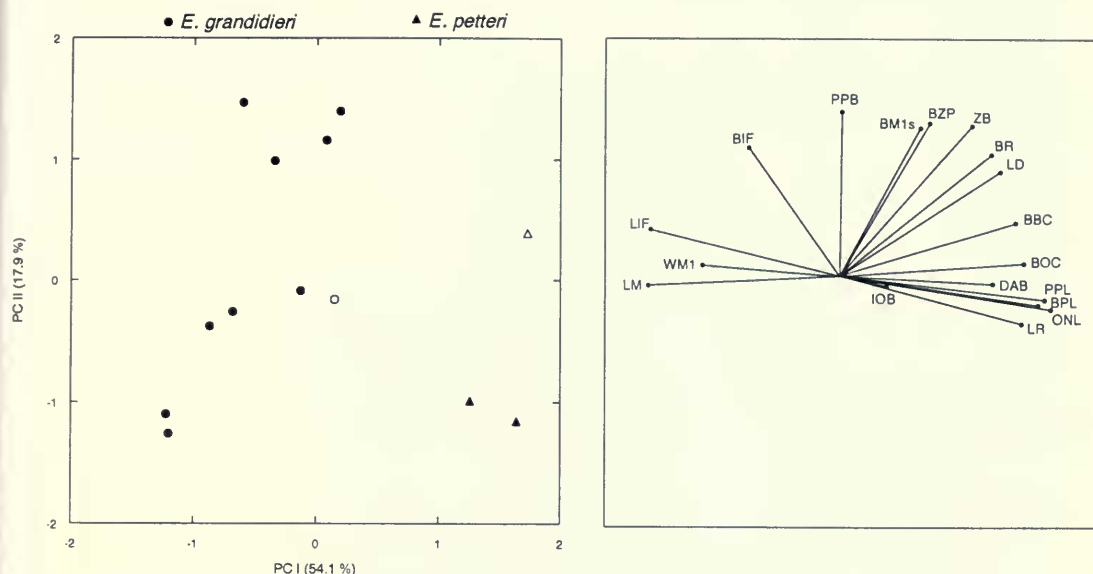


FIG. 11-7. Results of principal components analysis of 18 log-transformed craniodental variables measured on intact specimens of *Eliurus grandidieri* (N = 10) and *E. petteri* (N = 3). **Left**, Projection of individual scores onto the first two principal components (open symbols represent the type specimens). **Right**, Vectors of the 18 craniodental variables corresponding to the magnitude and direction of their loadings on the first and second principal components (also see Table 11-3).

tion in contrast to the wider zygomatic arches and shorter, broad rostrum typifying the skull of *E. grandidieri*. Furthermore, the absolutely and relatively larger incisive foramina and molars of the latter species enhance its robust appearance.

Such size and shape dissimilarities are reflected in ordination analyses of log-transformed measurements of all intact crania representing the two species. Most dimensions display large, positive correlations with the first principal component extracted and contribute to the hiatus between *Eliurus grandidieri* and *E. petteri* along that axis (Fig. 11-7, Table 11-3). Exceptions to this pattern include measurements of the molars (LM1-3 and WM1) and incisive foramina (LIF and BIF), which load negatively at moderate to strong levels on the first principal component (Table 11-3). The appreciable variation summarized by the second principal component, especially the spread among specimens of *E. grandidieri*, is plausibly attributed to age-related size increase in certain variables. This influence is particularly notable for many cranial breadths of the facial skeleton (such as BIF, BM1s, BR, BZP, and ZB), but less so for those dimensions measured across the braincase (BBC, BOC, and IOB). Age class, as an independent factor, significantly affects ( $F = 7.2$ ,  $P = 0.02$ , and  $df = 7$ ) the dispersion of PC II scores

among specimens of *E. grandidieri* (not calculable for the small sample of *E. petteri*).

### The Larger White-tailed Species

Among the five species of *Eliurus* collected within the RS d'Anjanaharibe-Sud, the second species with a white caudal tuft is unmistakable by virtue of size alone, e.g., the big hindfoot (HF > 32 mm) and generously proportioned skull (ONL > 42 mm). Seven examples (only four adults with skulls) of this distinctive form were obtained from the transect stations at 875 and 1260 m. A white caudal tuft characterizes samples of *E. tanala*, another large species so far known from midelevation humid forest (455–1625 m) that stretches from the Réserve Naturelle Intégrale (RNI) d'Andringitra to the vicinity of Lac Alaotra (Carleton, 1994; Goodman & Carleton, 1996). On the other hand, such robust dimensions equally recall those of *E. ellermani*, a dark-tailed form recently described by Carleton (1994) on the basis of two specimens from northeastern Madagascar (type locality = Hiaraka, see below).

The pelage and cranial attributes observed in the series from the RS d'Anjanaharibe-Sub raise doubts about the conservatism of certain features ad-

TABLE 11-3. Results of principal component analysis and one-way ANOVA performed on 18 log-transformed craniodental dimensions of specimens of *Eliurus grandidieri* (N = 10) and *E. petteri* (N = 3) (see also Fig. 11-7).

Variable	Correlations		F (species)
	PC I	PC II	
ONL	0.96	-0.15	76.1***
ZB	0.61	0.70	0.7
BBC	0.80	0.25	4.8
IOB	0.21	-0.05	0.0
LR	0.83	-0.22	18.7**
BR	0.69	0.57	2.0
PPL	0.94	-0.11	37.6***
LBP	0.91	-0.13	20.9**
LIF	-0.87	0.22	16.4**
BIF	-0.42	0.60	8.0*
LD	0.76	0.49	4.9*
BM1s	0.37	0.69	0.0
PPB	0.01	0.77	0.1
DAB	0.70	-0.03	9.0*
BZP	0.41	0.71	0.3
BOC	0.84	0.06	10.9**
LM1-3	-0.88	-0.04	32.7***
WM1	-0.63	0.05	12.4**
Eigenvalue	0.027	0.009	
% Variance	54.1	17.9	

\*  $P \leq 0.05$ ; \*\*  $P \leq 0.01$ ; \*\*\*  $P \leq 0.001$ .

vanced as diagnostic of *Eliurus ellermani* and its status as a species distinct from *E. tanala*. We explore these questions in this section in order to provide a firm identification of the larger white-tailed species. In addition to the two known individuals of *E. ellermani*, the following five series (OTUs) of *E. tanala* were consulted to broaden the comparative scope and estimate of infraspecific variation (see Appendix 11-1 for catalog numbers and specific locality data): RS d'Analamazaotra (N = 17), Parc National (PN) de Ranomafana (N = 18), Vinanitelo (N = 3, including the holotype), RNI d'Andringitra (N = 14), and RNI d'Andohahela (N = 16).

MORPHOLOGICAL AND MORPHOMETRIC COMPARISONS—Carleton (1994: p. 39) framed the diagnosis of *Eliurus ellermani* on the combination of the form's robust size and dark caudal tuft.

"A large (ONL = 42–44 mm, DHF = 33–34 mm) species of *Eliurus* that resembles a robust version of *E. tanala* except with the tail brush completely dark to the tip; skull stoutly constructed, especially as seen in its broader interorbit, braincase, and expanse of zygomatic arches."

Based on their uniform possession of a white tail tuft (ranging from 12 to 45 mm long on three skins), the RS Anjanaharibe-Sud series agrees with individuals of *Eliurus tanala* and fails to meet an important criterion in the definition of *E.*

*ellermani*. However, their resemblance to *E. ellermani* in other traits is remarkably fine. With regard to size, linear dimensions of the four adults circumscribe those of the two *E. ellermani* specimens (Table 11-4) and average larger than typical *E. tanala* in most aspects (Table 11-6). Still, they can be matched by individuals of the latter species from other localities, particularly those from around the RS d'Analamazaotra (Périnet and Lohariandava). Also, the underparts of the RS Anjanaharibe-Sud animals are monocolored, a dingy creamy white to creamy buff from chin to inguinal (unlike the bright white venter of *E. petteri*), and contrast sharply with the dark grayish brown of the dorsum. This color pattern conforms to the holotype of *E. ellermani* (MNHN 1981.871), but ventral hairs of the paratype (BM(NH) 47.1623) exhibit some basal gray banding to give a slightly darker cast. In addition to bigness and fur color, the seven RS Anjanaharibe-Sub specimens share a number of qualitative traits with *E. ellermani*, namely, the coarsely defined caudal scutellation, fenestrated bony palate, nearly occluded subquamosal fenestra and correspondingly broad hamular process, and a pronounced capsular process terminating high on the mandibular ramus. Examples of *E. tanala* also display the same character suite (Carleton, 1994).

TABLE 11-4. Comparison of selected external and craniodental measurements of the holotype (MNHN 1981.871) and paratype (BMNH 47.1623) of *Eliurus ellermani* with the larger white-tailed *Eliurus* from the RS d'Anjanaharibe-Sud, here assigned to *E. tanala* (N = 4-5).\*

Variable	<i>E. ellermani</i>		<i>E. tanala</i>
	Holotype	Paratype	Anjanaharibe-Sud
TOTL			361.5 ± 16.1 342.0-381.0
HB	152.0		167.8 ± 4.3 163.0-174.0
TL	177.0		187.2 ± 17.3 158.0-203.0
HF	35.0		33.3 ± 0.5 33.0-34.0
DHF	34.0	33.0	34.0, 35.0
WT			105.9 ± 12.0 96.5-120.0
ONL	43.8		44.1 ± 1.2 43.0-45.7
ZB	18.8	20.6	21.1 ± 0.5 20.3-21.5
BBC	15.2	15.7	15.4 ± 0.3 14.9-15.7
IOB	6.3	6.3	5.9 ± 0.2 5.5-6.0
LR	15.1	16.1	15.9 ± 0.8 14.8-16.6
BR	8.1	8.3	7.6 ± 0.4 7.2-8.0
PPL	15.5		15.2 ± 0.3 14.7-15.5
LBP	9.2	10.7	10.5 ± 0.7 9.7-11.4
LIF	5.8	5.4	5.7 ± 0.3 5.3-6.0
BIF	2.3	2.2	2.1 ± 0.1 2.0-2.3
LD	13.4	13.4	13.9 ± 0.6 13.1-14.5
BM1s	8.4	7.9	8.3 ± 0.3 8.0-8.6
DAB	5.1	5.3	5.3 ± 0.2 4.9-5.5
BZP	4.0	4.1	4.2 ± 0.1 4.1-4.3
BOC	9.3		9.2 ± 0.4 8.7-9.8
LM1-3	5.82	5.58	5.92 ± 0.25 5.51-6.22
WM1	1.61	1.63	1.65 ± 0.07 1.58-1.75

\* Sample statistics include the mean ± 1 SD and the observed range.

Nor do covariation patterns revealed in ordinations of craniodental data supply clear-cut evidence for specific separation of the RS Anjanaharibe-Sud animals from the holotype of *Eliurus ellermani* or from examples of *E. tanala*. The first two principal components extracted summarized 41.8 and 11.6% of sample variation, respectively,

but divulged no taxonomically meaningful discrimination among the population samples (results not figured); indeed, age class (three classes) as a post hoc explanatory effect influenced the dispersion of individual scores along the first component as strongly ( $F = 9.3$ ,  $P \leq 0.001$ , and  $df = 58$ ), as did membership in the six OTUs ( $F = 4.2$ ,

$P \leq 0.01$ , and  $df = 55$ ). In like manner, discriminant function analysis of the six population samples produced no discrete subdivisions that suggest specific-level differentiation. Plots of the first two canonical variates portray ambiguous scatter of the data points and appreciable overlap among the six OTUs (Fig. 11-8); loadings of the original variables are generally positive but low to moderate in strength (Table 11-5); and  $F$  values derived from one-way ANOVAs for OTU effects, although significant for many variables ( $df = 55$ ), are generally small (Table 11-5). Trenchant contrasts of size and/or shape, at magnitudes indicative of specific divergence among our six OTUs, are not apparent from this collection of results.

What interpretable structure does emerge from discriminant analysis suggests a weak size cline, from smaller in the south (Andohahela) to larger in the north (Anjanaharibe-Sud). Such an interpretation is consistent with the array of group centroids along the first canonical variate (Fig. 11-8), the geographic associations of population samples generated from Mahalanobis distances among their centroids (Fig. 11-9), and differences among the means of individual variables (Tables 11-4 and 11-6). Although clearly the largest in average size among the samples analyzed, the specimens from RS Anjanaharibe-Sud do not appear inherently different from those of *Eliurus tanala* from farther south. Furthermore, based on these analytical results alone, the type specimen of *E. ellermani* (MNHN 1981.871) appears as another example of the larger-bodied populations that inhabit the northern sector of Madagascar. According to posterior probabilities of group membership, the holotype of *E. ellermani* actually clusters ( $P = 0.95$ ) with the series from the RS d'Analamazaotra instead of the geographically closer RS d'Anjanaharibe-Sud (Fig. 11-8).

**SUMMARY AND EMENDED DIAGNOSIS**—The specimens of large, white-tailed *Eliurus* from the reserve are provisionally assigned to *E. tanala*. An increase in size, apparently clinal, is observed in populations of *E. tanala* from the RNI d'Andohahela (24.6°S) to the vicinity of the RS d'Analamazaotra (18.5°S) and finds its most robust expression, we hypothesize, in these northern highlands, as represented by the individuals from the RS d'Anjanaharibe-Sud. Moreover, invasive patches of cream-colored hairs on the venter occur sporadically in the series from the RS d'Analamazaotra and PN de Ranomafana; those from the RNI d'Andringitra and RNI d'Andohahela uniformly retain the medium gray underparts typical of *E. tanala*. Dominance or fixation of this chromatic variant may be expected in isolation, such as popu-

lations in the northern highlands separated from the main distribution of *E. tanala* along the eastern flanks of the Central High Plateau. Perhaps it is relevant that certain northern samples of *E. webbi*, whose distribution parallels that of *E. tanala* in eastern forest, although at lower elevations, also exhibit a high proportion of individuals with a creamy venter (Carleton, 1994). Finally, as circumstantial argument, we note that the altitudinal and habitat stratifications between the large, white-tailed species (875 and 1260 m) and *E. webbi* (only at 875 m) in the RS d'Anjanaharibe-Sud conform with the relationship documented for the two species farther south. Populations of *E. tanala* typically occupy middle montane associations, with most records coming from 800 to 1600 m, whereas those of *E. webbi* inhabit lowland rain forest, usually between sea level and 800 m. Overlap and syntopy of the two have been documented within an altitudinal band from 450 to 875 m (Carleton, 1994; Goodman & Carleton, 1996; Chapter 12).

An immense swath of unsampled territory still exists between Lac Alaotra, the previous northernmost report of *E. tanala*, and the RS d'Anjanaharibe-Sud. Surveys within this region would illuminate the nature of cranial and pelage variation and resolve any taxonomic uncertainty regarding our allocation of the large, white-tailed species.

In rendering this specific identification, we perforce remove exceptional size from the differential diagnosis of *Eliurus ellermani*. At present, we prefer to retain *E. ellermani* as a species, although its distinction from *E. tanala*, if it proves distinct, now rests solely on the possession of a dark tail tuft. By so narrowly amending the diagnosis of *E. ellermani*, the nature of contradictory evidence required to falsify its specific status is made more explicit. Two attendant considerations advise such a conservative course. For one, the type locality of *E. ellermani* was mistakenly located by Carleton (1994), as explained in the next section, and should be revisited to obtain new material. For another, coloration of the distal tail has proven to be a highly reliable trait for discriminating individuals of *E. tanala* and *E. webbi* elsewhere in Madagascar (Carleton, 1994). Also, the presence or absence of a contradistinctive tip is complemented, as with *E. petteri* and *E. grandidieri*, by other cranial differences that serve to separate the species. That is to say, we have not found the combination of cranial features that characterize *E. webbi* in a specimen with a white-tipped tail, except in instances of natural caudal injury and hair regeneration around the stump. Additional



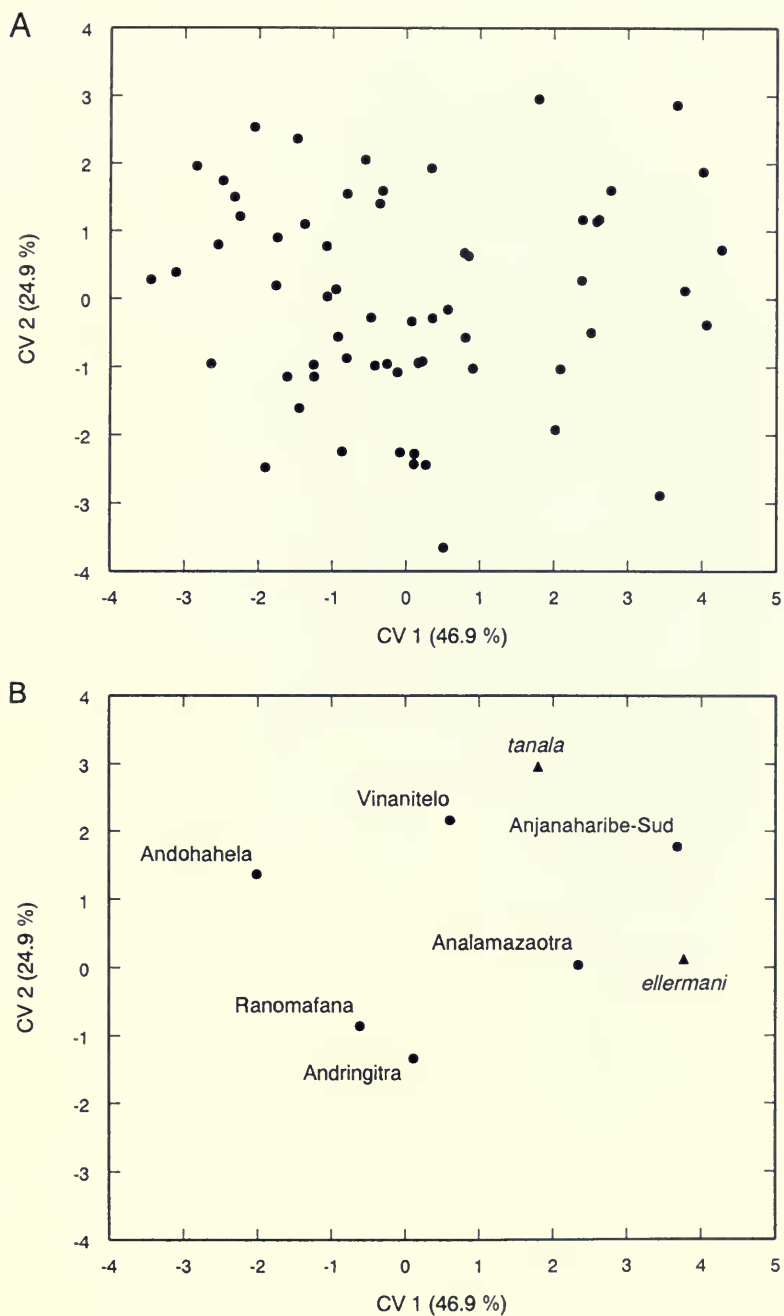


FIG. 11-8. Results of discriminant function analysis performed on 18 log-transformed craniodental variables, as measured on 62 intact specimens representing six OTUs of *Eliurus tanala*. **Top**, Projection of individual scores onto the first two canonical variates extracted. **Bottom**, projection of OTU centroids onto the first two canonical variates; closed triangles signify the type specimens of *E. ellermani* and *E. tanala*. See Table 11-5 and Figure 11-9.

TABLE 11-5. Results of discriminant function analysis and one-way ANOVA performed on 18 log-transformed craniodental dimensions of 61 specimens representing six OTUs of *Eliurus tanala* (see also Figs. 11-8, 11-9).

Variable	Correlations		F (OTU)
	CV 1	CV 2	
ONL	0.52	0.28	4.3**
ZB	0.35	0.41	3.2*
BBC	0.25	0.53	3.5**
IOB	0.13	-0.06	1.1
LR	0.21	0.14	3.0*
BR	0.50	0.26	3.0*
PPL	0.37	0.19	1.8
LBP	0.38	0.30	4.8**
LIF	0.17	0.16	0.4
BIF	-0.23	-0.71	6.5**
LD	0.40	0.31	3.9**
BM1s	0.40	0.30	2.8*
PPB	0.59	-0.01	5.5***
DAB	-0.10	0.15	1.3
BZP	-0.11	0.39	3.4**
BOC	0.76	-0.10	8.9***
LM1-3	0.30	-0.19	1.6
WM1	0.41	0.24	2.4*
Eigenvalue	3.05	1.0	
Canonical correlation	0.87	0.79	
% Variance	46.9	24.9	

\*  $P \leq 0.05$ ; \*\*  $P \leq 0.01$ ; \*\*\*  $P \leq 0.001$ .

collecting at the corrected type locality should answer the question of whether the two specimens that formed the basis of *E. ellermani* are just extreme variants within *E. tanala* or indeed represent a valid species.

TYPE LOCALITY OF *ELIURUS ELLERMANI*—Diagnosis of this form was based on two specimens,

the holotype (MNHN 1981.871), collected by R. Albignac at Hiaraka, 850 m, in January 1968, and a paratype (BM(NH) 47.1623), collected by C. S. Webb near Lohariandava, 13 mi (21 km) north of Rogez, 1300 ft (400 m), on 10 December 1939. Carleton (1994) located the type locality Hiaraka as 40 km northwest of Maroantsetra, at approxi-

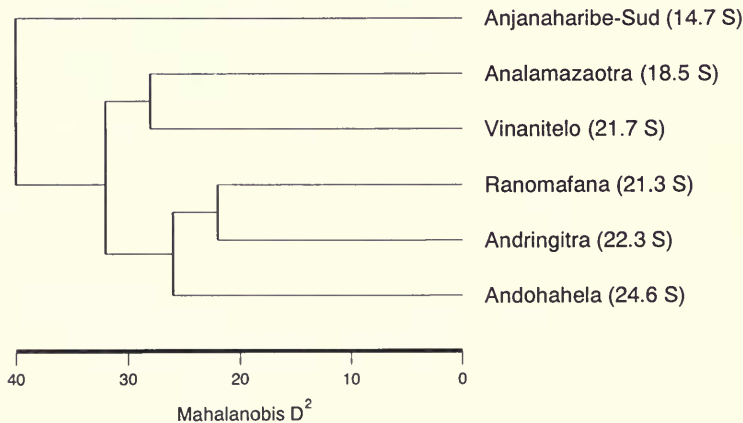


FIG. 11-9. Phenogram produced from clustering (UPGMA) of Mahalanobis' distances among centroids of six population samples of *Eliurus tanala* (degrees of S latitude indicated in parentheses). Associations among samples suggest a gradient in size, from smaller in the south (RNI Andohahela) to larger in the north (RS d'Anjanaharibe-Sud). See also Figure 11-8.

TABLE 11-6. Comparison of selected craniodental measurements for three samples of *Eliurus tanala*.\*

Variable	Andohahela 24.6°S (N = 15)	Ranomafana 21.3°S (N = 18)	Analamazaotra 18.5°S (N = 9-16)
ONL	40.4 ± 1.3 37.7-42.6	41.1 ± 1.5 38.5-43.8	41.3 ± 1.6 38.8-44.1
ZB	19.8 ± 0.7 17.6-20.6	19.3 ± 0.7 18.3-20.6	19.8 ± 1.1 17.1-21.2
BBC	14.9 ± 0.3 14.3-14.9	14.7 ± 0.3 13.9-15.5	14.8 ± 0.3 14.4-15.3
IOB	5.8 ± 0.2 5.5-6.1	5.9 ± 0.3 5.6-6.8	6.0 ± 0.2 5.6-6.4
LR	14.6 ± 0.6 13.5-15.5	14.8 ± 0.7 13.3-15.9	14.5 ± 0.8 13.4-16.4
BR	7.2 ± 0.3 6.6-7.8	7.1 ± 0.4 6.6-7.8	7.4 ± 0.3 6.8-7.9
PPL	14.3 ± 0.6 12.9-15.2	14.4 ± 0.6 13.2-15.5	14.7 ± 0.8 12.9-15.7
LBP	9.3 ± 0.4 8.3-9.9	9.2 ± 0.4 8.2-10.1	9.5 ± 0.6 8.7-11.0
LIF	5.5 ± 0.3 4.9-6.1	5.5 ± 0.4 4.9-6.1	5.5 ± 0.5 4.1-6.4
BIF	2.2 ± 0.1 2.1-2.4	2.4 ± 0.1 2.1-2.6	2.2 ± 0.2 1.9-2.5
LD	12.4 ± 0.5 11.2-13.1	12.4 ± 0.6 11.0-13.6	12.7 ± 0.7 11.1-13.7
BM1s	7.9 ± 0.2 7.5-8.3	7.9 ± 0.2 7.6-8.6	8.1 ± 0.3 7.6-8.6
PPB	5.1 ± 0.3 4.7-5.7	5.3 ± 0.3 4.7-5.9	5.4 ± 0.3 4.7-5.9
DAB	5.4 ± 0.1 5.1-5.6	5.2 ± 0.2 4.9-5.5	5.3 ± 0.1 4.9-5.5
BZP	4.0 ± 0.2 3.5-4.4	3.9 ± 0.3 3.4-4.7	3.8 ± 0.2 3.6-4.2
BOC	8.5 ± 0.3 7.9-9.0	8.6 ± 0.2 8.0-9.1	9.0 ± 0.2 8.7-9.2
LM1-3	5.66 ± 0.22 5.17-6.11	5.75 ± 0.13 5.52-5.99	5.80 ± 0.20 5.43-6.21
WMI	1.54 ± 0.07 1.36-1.64	1.53 ± 0.05 1.42-1.68	1.62 ± 0.09 1.43-1.79

\* Sample statistics include the mean ± 1 SD and the observed range. See Appendix 11-1 for exact localities and museum numbers.

mately 15°10'S and 49°30'E, following the geographic interpretation of MacPhee (1987).

The place name Hiaraka, however, is a common one in northeastern Madagascar, and we here present information that corrects the type locality erroneously reported for *Eliurus ellermani*. The original tag attached to the skin of MNHN 1981.871 vaguely localizes Hiaraka as "near" Maroantsetra but provides no specific distance. Another nearby Hiaraka is situated on the Masoala Peninsula, just across the Baie d'Antongil from Maroantsetra, about 18 km in an east-southeastern direction. Low mountains, with peaks to 1000-1200 m and with relatively intact forest, occur just inland from this Hiaraka, a small beach enclave currently es-

tablished for tourism. Andre Peyrieras has organized the visits of numerous French biologists to this area, including the 1968 mission of Roland Albignac (Peyrieras, pers. comm.). Hiaraka, located at about 15°30'S and 49°56'E (*sensu* Langrand & Sinclair, 1994), has also been an important locality for insect collecting (Viette, 1991).

Therefore, we amend the type locality of *Eliurus ellermani* Carleton (1994) to the following: Madagascar, Toamasina Province, near Hiaraka, about 18 km ESE of Maroantsetra, 850 m, coordinates about 15°30'S, 49°56'E. Two other species from Hiaraka, as reported by Carleton and Schmidt (1990), were also collected by Albignac in the same general period, an *E. minor* (MNHN

1981.870) in August 1967, no elevation given, and one *Nesomys* [*rufus*] *audeberti* (MNHN 1981.872) in May 1968 at 400 m. With elimination of these records, we cannot reliably associate any nesomyine with the Hiaraka located about 40 km northwest of Maroantsetra, a place also known as Bevato and visited by the Mission Zoologique Franco-Anglo-Américaine (see Archbold, 1930; Goodman, 1995).

## The Small *Eliurus*-Like Species

The last issue of taxonomic identity concerns a small, gray, mouselike rodent found in lush, mossy forest at 1950 m just below the summit (Fig. 11-10). Although murine in superficial appearance, examination of the animal's bodily proportions and hindfoot conformation in the field suggested an elfin form of *Eliurus* that lacks a caudal tuft. Subsequent study of its cranium and dentition in the museum revealed other features distinct from those of that genus. Although only three specimens of this small rodent were captured during the 1994 survey of the RS d'Anjanaharibe-Sud, they are sufficient to establish not only that the species is new but also that it does not fit within the morphological limits of any known genus of Nesomyinae.

### *Voalavo*, new genus

TYPE SPECIES—*Voalavo gymnocaudus* Carleton and Goodman, described below as new.

DIAGNOSIS—A form of the murid rodent subfamily Nesomyinae (*sensu* Carleton & Musser, 1984; Musser & Carleton, 1993) characterized by small size (TOTL about 210–215 mm; HB about 86–90 mm) (in other nesomyines except *Monticolomys*, average HB  $\geq$  100 mm); tail appreciably longer than head and body, TL about 132–138% of HB (TL  $\leq$  HB in *Brachyuromys*, *Gymnuromys*, *Hypogeomys*, and *Nesomys*), without noticeable elongation of caudal hairs over distal half (distal tip penicillate in *Macrotarsomys*, a brushy tuft in *Eliurus*); hindfoot short (HF = 20–21 mm) and relatively broad, outer digits I and V comparatively long (hindfoot long and narrow, outer digits relatively short in *Gymnuromys*, *Macrotarsomys*, and *Nesomys*); hairs of ungual tuft surpassing tip of claw (tuft hairs shorter than claw in *Macrotarsomys*).

Cranium small (ONL = 26–27.5 mm, LM1–3 = 3.7–3.8 mm) and delicately built with slender,

nearly parallel sided zygomatic arches and narrow, hourglass-shaped interorbit; zygomatic plate narrow, notch indistinct (plate broader, zygomatic notch shallow to deep in other nesomyines except *Brachytarsomys*); squamosal–alisphenoid bones lacking vascular groove, stapedial and sphenofrontal foramina absent (groove and foramina present in *Macrotarsomys*, *Monticolomys*, and *Nesomys*); alisphenoid strut absent (strut present in *Brachyuromys*, most *Eliurus*, *Hypogeomys*, and *Nesomys*); ectotympanic bullae very small, like *Eliurus*, relatively wide ventromedial wedge of periotic exposed (bullae more inflated, narrow expanse of periotic visible in *Monticolomys*; bullae much larger, periotic mostly obscured in *Brachyuromys*, *Hypogeomys*, *Macrotarsomys*, and *Nesomys*); tegmen tympani reduced, not contacting squamosal (overlap with squamosal in *Brachytarsomys*, *Eliurus*, and *Gymnuromys*).

Entepicondylar foramen of humerus absent (foramen present in all other nesomyine genera except *Brachyuromys*).

Upper toothrows parallel (convergent anteriorly in *Brachyuromys*, divergent anteriorly in *Macrotarsomys* and *Monticolomys*); molars planar, surfaces configured as nearly transverse laminae, and incipiently high-crowned, approaching *Eliurus* (cheek teeth cuspidate and brachyodont in *Macrotarsomys* and *Monticolomys*, moderately hypsodont with distinct cusps in *Nesomys*); upper and lower third molars notably smaller than second molars (size of third molar approximately equal to second in *Brachyuromys*, *Eliurus*, *Hypogeomys*, and *Nesomys*; conspicuously larger than second molar in *Gymnuromys*); two laminae on lower third molar, lamination undefined on upper third molar (three on third molars of most *Eliurus*); mesoloph and mesolophids absent (present in *Gymnuromys* and *Nesomys*); posteroloph absent on upper first molar, present on upper second molar (posteroloph present on unworn M1–3 of *Eliurus*); upper molars with three roots and lowers with two (upper molars four-rooted in *Hypogeomys*).

MORPHOLOGICAL DESCRIPTION—The single known species is described below.

### *Voalavo gymnocaudus*, new species

(Figs. 11-10–11-18, Table 11-7)

HOLOTYPE—Field Museum of Natural History number 154040; skin, skull, and postcranial skeleton of adult male (original number SMG 7081), collected 25 November 1994 by S. M. Goodman.





FIG. 11-10. View of sclerophyllous montane forest at 1950 m, just below the summit of Anjanaharibe-Anivo. Trees in this high mountain zone are typically lower in height and thickly carpeted with mosses and epiphytes. The holotype (FMNH 154040) of *Voalavo gymnocaudus*, new genus and species, was collected in the Sherman live trap pictured here, positioned on a large horizontal limb approximately 3 m above the forest floor. (Photograph by S. M. Goodman.)

TABLE 11-7. Comparison of selected external and craniodental measurements of the holotype (FMNH 154040) and type series of *Voalavo gymnocaudus* with those representative of *Eliurus minor*.\*

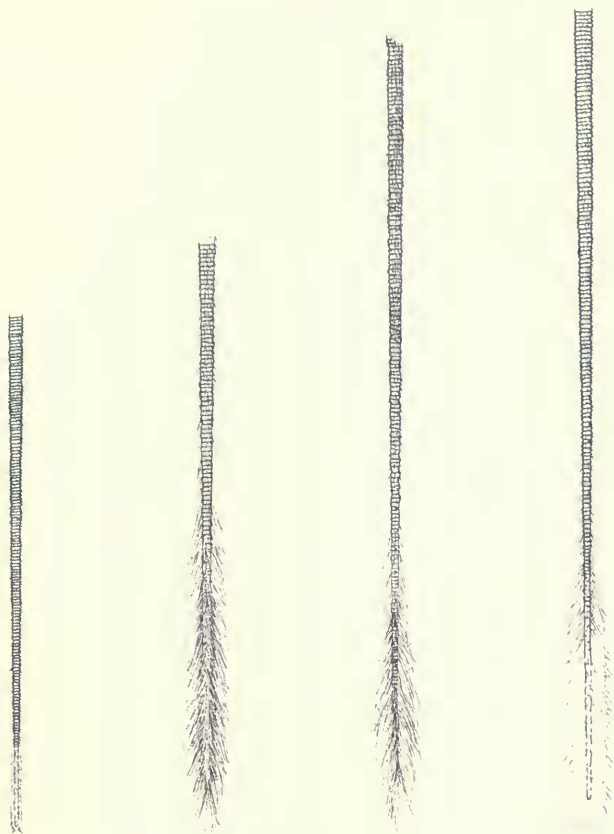
Variable	<i>Voalavo gymnocaudus</i>		<i>Eliurus minor</i> <sup>†</sup>
	Holotype	Type series <sup>‡</sup>	
TOTL	212.0	212.7 ± 1.1 212.0–214.0	231.5 ± 13.8 214.0–257.0
HB	86.0	87.7 ± 2.1 86.0–90.0	105.7 ± 6.5 95.0–116.0
TL	119.0	119.3 ± 0.6 119.0–120.0	125.5 ± 8.8 110.0–141.0
HF	21.0	20.7 ± 0.6 20.0–21.0	24.0 ± 1.1 22.0–26.0
WT	22.0	22.0 ± 1.5 20.5–23.5	33.5 ± 4.6 25.0–39.0
ONL	26.9	27.0 ± 0.1 26.9–27.1	30.1 ± 0.9 28.7–31.3
ZB	13.8	13.8 ± 0.2 13.7–14.0	15.0 ± 0.4 14.4–15.7
BBC	11.2	11.2 ± 0.1 11.1–11.3	12.0 ± 0.3 11.4–12.5
IOB	4.6	4.5 ± 0.1 4.4–4.6	4.9 ± 0.1 4.7–5.2
LR	9.7	9.3 ± 0.4 8.8–9.7	10.1 ± 0.5 9.2–10.8
BR	5.0	4.9 ± 0.1 4.8–5.1	5.5 ± 0.2 5.1–5.9
PPL	9.8	9.4 ± 0.2 9.3–9.8	10.7 ± 0.4 10.0–11.2
LBP	4.0	4.4 ± 0.3 4.0–4.7	6.2 ± 0.3 5.4–6.6
LIF	4.5	4.2 ± 0.3 3.9–4.5	3.9 ± 0.1 3.5–4.3
BIF	1.6	1.7 ± 0.1 1.6–1.8	2.0 ± 0.1 1.8–2.2
LD	7.5	7.5 ± 0.1 7.3–7.6	8.5 ± 0.3 7.8–9.1
BM1s	5.5	5.5 ± 0.2 5.2–5.7	6.0 ± 0.1 5.8–6.2
DAB	3.9	3.8 ± 0.1 3.7–3.9	4.5 ± 0.2 4.2–4.8
BZP	2.2	2.2 ± 0.05 2.1–2.3	2.5 ± 0.08 2.3–2.6
BOC	6.5	6.3 ± 0.1 6.1–6.5	6.8 ± 0.2 6.4–7.0
LM1-3	3.72	3.73 ± 0.04 3.70–3.79	4.18 ± 0.08 4.05–4.31
WM1	1.09	1.09 ± 0.04 1.04–1.12	1.14 ± 0.05 1.02–1.19

\* Sample statistics include the mean ± 1 SD and the observed range.  
† For external variables, N = 3 (FMNH 154040, 154041, and 154267); for cranial variables, N = 4 (FMNH 154040, 154041, 154267, and 156162).  
‡ Specimens (N = 11–13) from the vicinity of PN de Ranomafana. See Appendix 11-1 for provenance and museum numbers.

Standard measurements (in mm) from the skin tag of the type include TOTL, 212; HB, 86; TL, 119; HF (without claw), 21 (DHF as measured by M.D.C. with claw, 21.5); EL, 15; and WT (in g), 22.0. The animal is noted as having scrotal testes (7 × 5 mm) with slightly convoluted epididymi-

des, and the microhabitat is recorded as “In ‘elfin’ upper montane forest. Trap 3 m off ground on 28 cm diam. moss-covered limb of tree.” Both skin and skull are in good condition (Fig. 11-12).

TYPE LOCALITY—Madagascar, Province d’Antsi-



**Voalavo**

***E. minor***

***E. petteri***

***E. grandidieri***

FIG. 11-11. Development of caudal pilosity in *Voalavo gymnocaudus* (FMNH 154040: TL = 119 mm), new genus and species, and three species of *Eliurus*, *E. minor* (USNM 449247: TL = 130 mm), *E. petteri* (USNM 341825: TL = 178 mm), and *E. grandidieri*, new species (FMNH 154048: TL = 186 mm). Full lengths of caudal vertebrae are portrayed to the same scale. Note the sparsely furred tail of *Voalavo* and the elaboration of a terminal tuft on that of members of *Eliurus*.

ranana, Réserve Spéciale d'Anjanaharibe-Sud, 12.2 km WSW of Befingitra, 1950 m, 14°44.8'S, 49°26.0'E (as given by the collector).

REFERRED SPECIMENS—Province d'Antsiranana, RS d'Anjanaharibe-Sud, 12.2 km WSW of Befingitra, 1950 m, 14°44.8'S, 49°26.0'E; FMNH 154041: female, skin, skull, and postcranial skeleton, viscera saved; FMNH 154267: male, skull with whole carcass in fluid, western slope, c. 1300 m, 14°46'S, 49°26'E; FMNH 156162: male, skull with carcass in fluid; FMNH 156163: female, whole carcass in fluid.

FMNH 154041 and 154267 were also collected by S. M. Goodman, on 25 and 26 November 1994, as part of the same inventory. FMNH 156162 and 156163 were captured by Franco Andreone,

between 4 and 12 February 1996, as part of a herpetological survey on the western slopes of the same reserve.

DISTRIBUTION—At present only known from montane and sclerophyllous montane forest, 1300–1950 m, in the RS d'Anjanaharibe-Sud.

DIAGNOSIS—As for the genus, above.

MORPHOLOGICAL DESCRIPTION—Fur soft and short (6–7 mm on midrump), relatively thick and finely textured (based on FMNH 154040 and 154041). Cover hairs of dorsum tricolored, with basal band long, four-fifths or more of shaft length, and plumbeous gray, narrow subterminal band pale buffy, and abbreviated tip black; guard hairs thin and black, a little longer than cover fur, unnoticeable except on rump; combined effect of

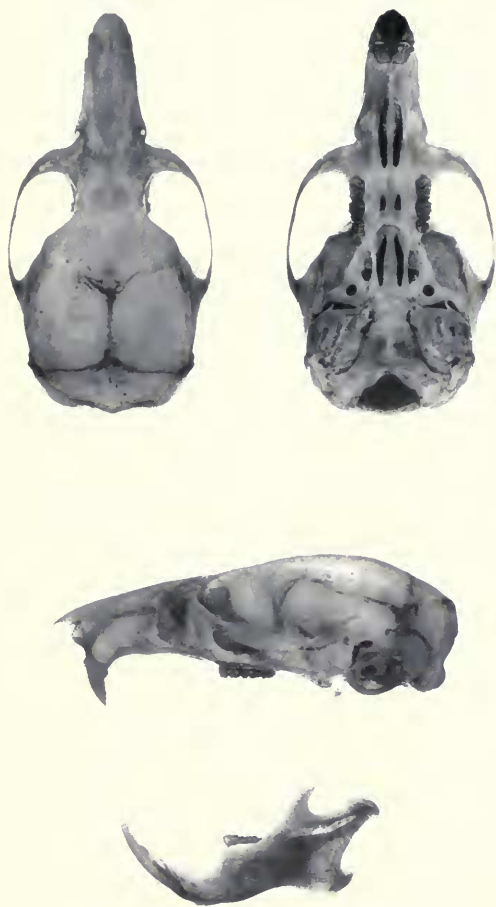


FIG. 11-12. Dorsal, ventral, and lateral views of the cranium and lateral view of the mandible of the holotype (FMNH 154040; ONL = 26.9 mm) of *Voalavo gymnocaudus*, new genus and species.

upperparts a dusky gray, more brownish gray on sides. Fur over ventral surface, from throat to groin, bicolored, with proximal three-quarters silver gray and tip white; mostly white to bases on chin; overall impression a dark gray ventrum not sharply contrasted with muted tones of dorsum. Mystacial vibrissae medium in length, the longest whiskers reaching the top of the pinnae when appressed to the skin; genal vibrissae small and inconspicuous. Pinnae short and rounded, thinly clothed externally and along rim with dark brown hairs, inner surface mostly naked. Tail long relative to head and body length (TL about 136% of HB), naked in gross appearance over proximal two-thirds and finely haired toward tip (Fig. 11-11); distal section not elaborated as pencil or terminal tuft; undersurface slightly lighter but dorsal-ventral bicoloration indiscernible. Epidermis

of tail gray, some light mottling underneath, scutellation fine, little obscured by hairs except near tip. Caudal hairs fine and short, about 1-2 mm long and spanning about two annulations; dorsal hairs colored deep brown over most of tail length, ventral hairs white to tip, but terminal 20-40 mm invested dorsally and ventrally with fine white hairs. Mammary number 6 (based on FMNH 154041 and 156163), distributed as one postaxial and two inguinal pairs (or one postaxial, one abdominal, and one inguinal pair *sensu* Voss & Carleton, 1993).

Tops of carpals, metacarpals, and phalanges furred in white; toes and most of metatarsus also white, dusky hairs extend over the tarsus and onto the proximal metatarsus; ungual tufts present but sparsely developed, the longest white hairs extending beyond end of claw; palmar and plantar surfaces naked. Palmar surface of manus with five prominent pads, consisting of three nearly contiguous interdigitals and the larger thenar and hypothenar, these approximately equal in size. Hindfoot relatively broad and short (Table 11-7), HF about 23% of HB, with claws on all digits. Outer digit V of hindfoot nearly as long as central digits (II-IV), the tip of its claw reaching to base of claw (ungual phalanx) of digit IV; claw of hallux extends to end of first phalanx of digit II. Plantar surface naked to heel and bearing six large, fleshy pads (Fig. 11-13); interdigital pads 1-4 positioned near one another at base of digits; hypothenar pad round and cushionlike, only slightly smaller than interdigitals and located just behind the level of interdigital 1; thenar also round to oval, situated near middle of tarsus-metatarsus, and a little larger than interdigital pads.

Cranium lightly constructed, delicate in appearance (Fig. 11-12). Rostrum narrow and moderately long (LR about 34% of ONL), tapering forward gradually from nasolacrimal capsules to end of nasals; anterior tips of nasals rounded to slightly pointed, extending beyond premaxillae and overhanging anterior nares; posterior margins blunt, terminating short of posterior limits of rostral processes of premaxillae. Zygomatic plate narrow, its anterior edge straight and set behind nasolacrimal capsule; dorsal notch indistinct; posterior border of plate positioned about equal to plane of anterior root of M1. Zygomatic arches thin and nearly parallel-sided over midportion, broadest at squamosal-jugal junction and weakly converging anteriorly; jugal relatively deep for size of skull, notably long as in other nesomyines, forming most of midspan of arch and distinctly



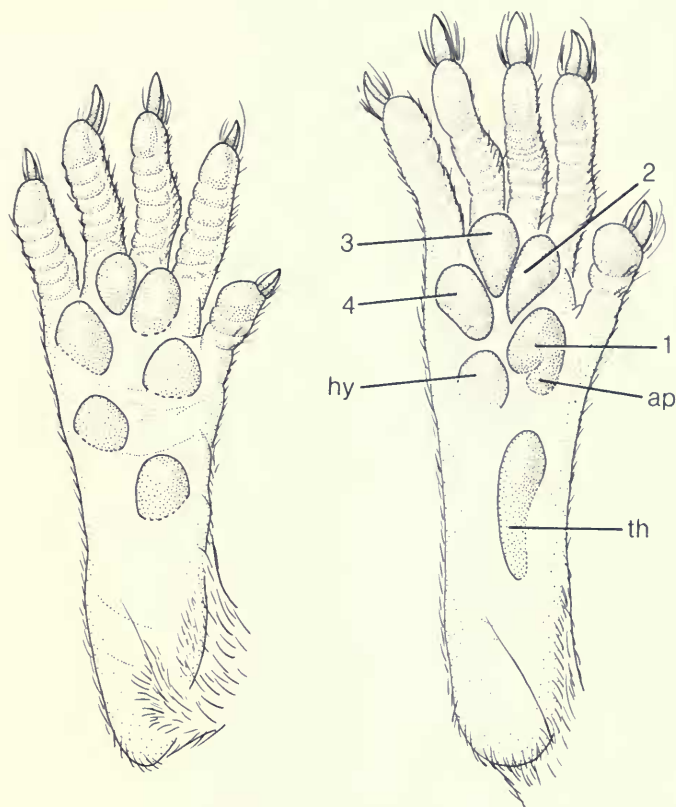


FIG. 11-13. Plantar view of the right hindfoot. **Left**, *Voalavo gymnocauidus* (FMNH 156162; HF = 21 mm), adult male from Antsiranana Province, RS d'Anjanaharibe-Sud. **Right**, *Eliurus minor* (USNM 449388; HF = 22 mm), adult male from Fianarantsoa Province, 3 km NNW of Vohiparara. 1-4 = interdigital pads 1-4; ap = accessory pad on interdigital 1; hy = hypothenar pad; and th = thenar pad. Note especially the contrast in size and shape of the thenar pad between *Eliurus* and *Voalavo*.

separating zygomatic processes of squamosal and maxillary.

Interorbital region short and narrow, exposing floor of orbits in dorsal view; amphoral (hour-glass-shaped), lacking supraorbital shelving and ridging; orbital projection of lacrimal small, proportioned as in *Eliurus*. Small rugosity developed on squamosal at rear of orbit, just behind squamosal-frontal suture, forming a low vertical ridge in adult specimens and imparting a squared appearance to anterior braincase. Neurocranium otherwise unmarked by temporal ridges or sagittal crest, smooth and gently rounded at lateral margins; frontoparietal suture defining a 90° angle at midsagittal juncture; interparietal large and wide, rhomboidal in outline but lateral apices not quite contacting squamosals (posterolateral corner of parietal and lateral exoccipital meet narrowly). Dorsal profile of skull conspicuously arched over calvarium, its highest point formed just posterior

to the frontoparietal junction, dorsal profile nearly straight over interorbit and rostrum.

Incisive foramina medium in length, spanning about 55% of diastema and terminating well in front of anterior root of first molars; foramina slightly wider at their midsection, gently convergent at either end but not acutely pointed. Palatal bridge relatively broad and smooth, devoid of corrugations, excrescences, or posteromedial spine; posterior palatine foramina relatively large but occurring as single pair of round to oval holes in maxillopalatine suture, about level with abutment of M1-M2 (foramina large and ovate in holotype, small and circular in others); posterior border of palate broadly rounded, situated even with middle of third molars, and lacking posterolateral palatal pits. Mesopterygoid fossa spacious and horse-shoe-shaped; sphenopalatine vacuities wide and long, exposing narrow span of basisphenoid-pre-sphenoid. Parapterygoid fossae slightly broader

than midsection of mesopterygoid fossa, relatively short and triangular in shape, recessed little relative to the plane of the hard palate; roof of parapterygoid fossae almost flat, incompletely ossified with wide fontanelle formed along medial border; fossae also pierced near posterolateral corner by partially occluded opening to alisphenoid canal, which lacks a vascular groove for passage of the infraorbital branch of the stapedia artery.

Ectotympanic bullae small; bullar volume comparable with that of most *Eliurus* species, with large posteromedial wedge of the periotic visible in ventral aspect; mastoid capsule similarly small and bulbous, fully ossified (no posterodorsal fontanelle); malleus typical of the parallel type, with knoblike orbicular apophysis. Tegmen tympani reduced, not overlapping with ventrolateral margin of squamosal; eustachian tube short and wide, not reaching tip of pterygoid process; carotid canal (passage of internal carotid artery) poorly defined as a shallow notch on the rear edge of the eustachian tube. Middle lacerate foramen spacious, its opening confluent with postglenoid foramen; postglenoid foramen medium, semicircular in outline, circumscribing an area about 1.5 times that of the smaller subsquamosal fenestra; hamular process of squamosal well defined and slender.

Alisphenoid strut absent, masticatory–buccinator and accessory oval foramina conjoined as one expansive opening. Sphenofrontal and stapedia foramina absent, vascular imprint lacking across inner surface of squamosal and alisphenoid bones, and posterior opening of alisphenoid canal irregularly formed, anatomical landmarks suggesting a derived carotid circulatory pattern involving loss of the supraorbital and infraorbital branches of the stapedia artery.

Coronoid process of dentary falcate, extending dorsad slightly above the condylar process; sigmoid notch moderately deep and ovate, concave emargination of angular notch unremarkable in size and shape. Alveolus of lower incisor extends posteriorly to level of coronoid process, notably below ventral rim of sigmoid notch; termination evident as slight bulge on ascending ramus but not protruding as capsular process. Superior and inferior masseteric ridges join anteriorly at obtuse angle, at level below anterior root of m1.

Axial skeleton (per FMNH 154040 and 154041) with 13 thoracic, seven lumbar, four sacral (two pseudosacral), and 38–39 caudal vertebrae. First rib articulates only with first thoracic vertebra, not contacting transverse process of seventh cervical. Neural spine of second thoracic vertebra notably

the tallest of the thoracic spines. Entepicondylar foramen of humerus absent.

Upper incisors somewhat delicate, asulcate, and nearly orthodont; enamel yellow to pale orange; face of lower incisors ornamented with close-set, parallel longitudinal ridges as in other nesomyines. Upper molar rows more or less parallel; molar crowns incipiently hypsodont, approaching *Eliurus*. Identity of individual cusps lost, occlusal surfaces planar, configured as slightly oblique to nearly transverse laminae; laminae number 3 on upper and lower first and second molars, 2 on lower third molar, laminae undefined on upper third molar; medial enamel connections (mures and murids) between individual laminae absent. First and second molars, both upper and lower, nearly equal in size (length and occlusal area); upper and lower third molars conspicuously smaller, roughly circular in outline, about one-third to one-half the size of the second molars. Three roots on each upper molar and two on each lower molar.

NOTES ON NATURAL HISTORY—All three specimens of *Voalavo gymnocauidus* obtained during the 1994 inventory were collected at the uppermost station of the elevational transect, at 1950 m, just below the summit of Anjanaharibe-Anivo (Fig. 1-1). The habitat at 1950 m may be generally categorized as sclerophyllous montane forest. Tree height in this high mountain zone is typically lower, and bryophytes and epiphytes profusely carpet plant and ground surfaces (Fig. 11-10); such physiognomic and floristic characteristics evoke the other common descriptors of this vegetational community, “elfin” or “mossy” forest. Although little rain fell during the brief visit in late November, the upper slopes around the 1950 m camp were usually shrouded in clouds, and mossy surfaces were drenched with moisture. The 1996 records of *V. gymnocauidus* from the western slopes of the RS d’Anjanaharibe-Sud, around 1300 m, suggest that the species may range more widely over moist montane forest within the reserve and perhaps elsewhere in the highlands of northern Madagascar. The extent of its distribution remains to be learned.

At 1950 m, the three examples of *Voalavo gymnocauidus* were trapped with individuals of *Eliurus majori* and *Nesomys rufus*, as well as the ubiquitous *Rattus rattus*. Its occurrence in montane forest as low as 1300 m indicates probable sympatry with other nesomyines like *E. grandidieri*, *E. minor*, *E. tanala*, and *Gymnuromys roberti*. Additional observations on ecology and re-

productive condition of the few specimens of *Voalavo* obtained are reported in Chapter 12.

**ETYMOLOGY**—The generic name *Voalavo* is a Malagasy word used generally for "rodent." The epithet *gymnocaudus* draws attention to the animal's apparently naked tail, a trait that readily separates the new genus from its presumed nearest generic ally, *Eliurus*, or tufted-tailed rats.

## Morphological Comparisons

Whether indexed by weight or by linear dimensions of the skin and skull, individuals of *Voalavo* *gymnocaudus* qualify as the smallest form of Nesomyinae so far known, smaller even than *Monticolomys koopmani*, another montane taxon recently described from the Central High Plateau (Carleton & Goodman, 1996). The diminutive size and generalized mouselike appearance easily separate *Voalavo* from the larger, morphologically distinctive forms like *Brachytarsomys*, *Brachyromys*, *Gymnuromys*, *Hypogeomys*, *Macrotarsomys*, and *Nesomys* (e.g., see descriptions, measurements, and/or keys in Ellerman, 1941, 1949; Petter, 1972, 1975; Carleton & Goodman, 1996; Goodman & Carleton, 1996; and Chapter 12 this volume). Although discrimination of the new genus from most nesomyines is unproblematic, species of *Eliurus* possess several traits that suggest their close affinity to *Voalavo*. Detailed comparison and contrast of these two genera follow.

**EXTERNAL FORM**—Examples of *Voalavo* and *Eliurus* resemble one another in many aspects of their external appearance and bodily proportions. In view of the pelage variation observed within *Eliurus*, nothing about the texture, color, or degree of dorsal-ventral countershading in *Voalavo* stands apart as inherently different. The genera display the same general foot morphology, including the position and number of pads on the fore- and hindfeet, comparative lengths of the metapodials and phalanges, and presence of ungual tufts. In particular, the development of the fifth toe is comparable in both and approximates the length of the three central digits (Fig. 11-13). Females of *Voalavo* and *Eliurus* possess six mammae, arranged as one postaxial and two inguinal pairs.

The absence of a terminal caudal tuft constitutes visually obvious means for segregating specimens of *Voalavo* from those of *Eliurus*, all species of which exhibit a pronounced elongation of hairs over the distal one-third to one-half of the

tail length (Carleton, 1994). Although the tail of *Voalavo* appears almost naked when inspected superficially, careful or microscopic examination reveals a fine cover of short hairs. Near the tip, the caudal hairs lengthen (maximum 1–2 mm long) and may be grossly discernable (Fig. 11-11). As conveyed by their vernacular name, tufted-tailed rats, the distal caudal plume borne by specimens of *Eliurus* is lush and readily discernible, the individual hairs ranging from 8 to 15 mm long, depending on the species. The white hairs and pale epidermis that accent the caudal tip of *Voalavo* also characterize some species of *Eliurus*, such as *E. grandidieri* and *E. tanala*, although the bicolored tips of the latter are more obvious because of the abrupt elongation of distal hairs (Fig. 11-11). The tail of *Voalavo* is long for the size of body (TL about 136% of HB), equal in proportion to the longest known among species of *Eliurus* (namely, *E. grandidieri* and *E. petteri*); however, most *Eliurus* have comparatively shorter tails (115–120% of HB).

A less dramatic but equally consistent generic dissimilarity involves the conformation of the plantar pads of the hindfoot. In members of *Eliurus*, the medial tarsal pad (thenar) is conspicuous among the plantar complement of six, being strikingly longer, obovate in shape, and generally twice the area of the anterior pads; the thenar in examples of *Voalavo* is circular in outline and more or less equal in size to the hypothenar and interdigitals (Fig. 11-13). Small, incompletely formed pads regularly occur at the outer border of the first and sometimes the fourth interdigital pads of *Eliurus* (see also Carleton, 1994: Fig. 2); such subdivisions of the primary interdigital pads are not defined on any individuals of *Voalavo*, including the three fluid-preserved specimens. Although distributed similarly over the plantar surface, the pads of both the manus and pes are larger, more bulbous, and nearly contiguous in *Eliurus*.

**CRANIUM AND MANDIBLE**—Skulls of *Voalavo* and *Eliurus* are fundamentally alike in proportions and general appearance, their facial skeleton moderately long (LR about 34–36% of ONL), the interorbital region amphoral and devoid of supraorbital ridges, and the braincase smooth and gently contoured. In both genera, a narrow flange of the alisphenoid bone extends dorsally above the level of the orbitosphenoid and contributes appreciably to the rear wall of the orbit. The ventral aspect of their crania displays as many similarities: the palatal bridge in



both is basically flat and featureless, the parapterygoid fossae shallow and equally perforated, and the mesopterygoid fossa wide, enclosing spacious sphenopalatine vacuities. The small ectotympanic bullae of *Voalavo*, their formation relative to the exposure of the periotic and the forward extension of the eustachian tube relative to the pterygoid process, resemble the condition observed in examples of *Eliurus*. The two genera lack certain cranial foramina (stapedial and sphenofrontal) and arterial traces (squamosal–alisphenoid and parapterygoid grooves), which together indicate a derived carotid circulatory pathway (Bugge, 1970; Carleton & Musser, 1989).

In other cranial characters, the condition observed in *Voalavo* matches one state within the array of variation so far documented among species of *Eliurus*. The four crania of *Voalavo* exhibit union of the masticatory–buccinator and accessory oval foramina (strut of the alisphenoid bone missing). Almost all specimens of almost all species of *Eliurus* possess the bony pillar that separates these foramina as discrete openings at the base of the alisphenoid; only the three known examples of *E. petteri* and a few *E. grandidieri* lack an alisphenoid strut. The postglenoid foramen and subsquamosal fenestra, and the bony hamular partition between them, are clearly defined in *Voalavo*; patency of the subsquamosal fenestra and concomitant definition of the hamular process of the squamosal are more variable among species of *Eliurus*, clearly marked in most but nearly occluded in some (especially *E. tanala*). The presence of a rugosity on the rear orbital wall, expressed as a low vertical ridge in fully adult *Voalavo*, is atypical of *Eliurus*, in which the rear orbital wall is usually smoothly contoured. It is common in certain species, however, particularly samples of *E. majori* and *E. minor*, and appears to vary with size and age as with other osseous features associated with muscle origins. By its position and vertical orientation, this rugosity recalls the postorbital ridge described for *Holochilus* (Voss & Carleton, 1993: Fig. 9) but is never so large or pronounced as to obscure the frontosquamosal suture in lateral view. The incisive foramina of *Voalavo* are long relative to the diastemal span, equaling the longest observed within *Eliurus* (*E. majori* and *E. penicillatus*) and clearly exceeding the size characteristic of most species (Fig. 11–14). The lower incisor of *Voalavo* has a relatively short alveo-

lus and correspondingly indistinct capsular process, features that resemble those of certain *Eliurus* (*E. grandidieri*, *E. majori*, and *E. petteri*); however, most species of the latter genus possess a longer incisor that terminates as a distinct lateral mound just below or at the sigmoid notch.

The regions of the auditory bullae and anterior zygoma present trenchant contrasts between the crania of *Voalavo* and *Eliurus*. The tegmen tympani, an anterior flange of the periotic that roofs the epitympanic recess, continues forward in examples of *Eliurus* to firmly contact the squamosal bone. The margin of the squamosal bows posteroventrally where the lip of the tegmen tympani overlaps, and their articulation forms an osseous division between the openings of the postglenoid and middle lacerate foramina (Fig. 11–15). The tegmen tympani is notably shorter in specimens of *Voalavo*, such that the postglenoid and middle lacerate foramina are broadly confluent. Although the subsquamosal fenestrae remain open in most *Eliurus*, they are typically smaller and cleftlike, exposing the lateral wall of the periotic but none or little of the lumen of the braincase. The hamular process of the squamosal thus appears as a short, stout strut adnate to the mastoid capsule. In the sample of *Voalavo*, the subsquamosal fenestrae are more spacious, revealing the lumen of the braincase and, together with the postglenoid foramen, delineating a slim hamular process (Fig. 11–15).

The configuration of the anterior portion of the zygomatic arch differs substantially (Fig. 11–16). In species of *Eliurus*, the zygomatic plate is uniformly wider, its anterior edge slightly overlapping the nasolacrimal capsule and forming a discrete zygomatic notch. In *Voalavo gymnocaudus*, the plate is narrower and its straight forward edge does not extend beyond the rear margin of the nasolacrimal capsule; accordingly, the anterodorsal rim of the zygoma is scarcely emarginated where the free dorsal edge of the narrow plate meets the superior ramus of the infraorbital canal. Although the zygomatic plate in *Eliurus* is relatively narrow among Nesomyinae, for instance, compared with species of *Brachyuromys* and *Nesomys*, the dorsal notch is nonetheless consistently defined, albeit shallow. Among nesomyines, *Voalavo*, in its rudimentary expression of a notch, surpasses only the construction found in *Brachytarsomys*,



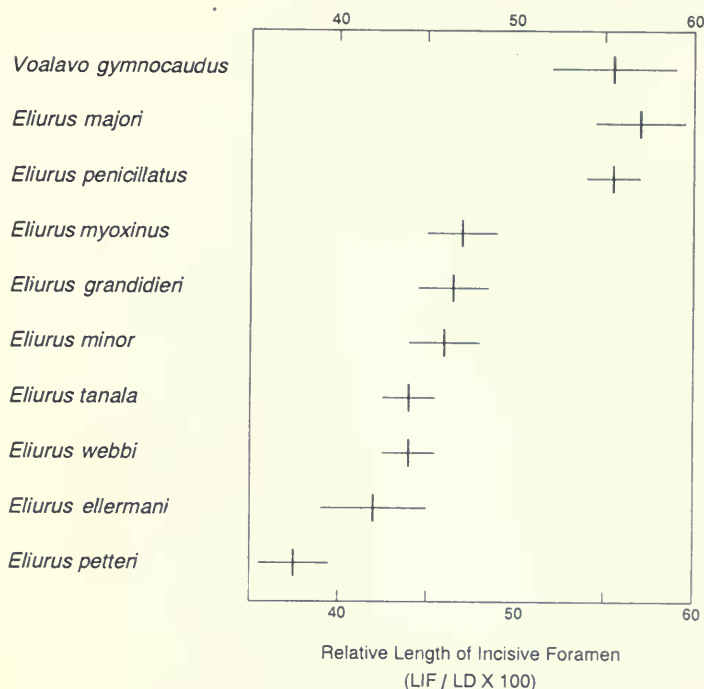


FIG. 11-14. Relative length of the incisive foramen in *Voalavo gymnocaudus* and species of *Eliurus*. Relative length expressed as the ratio of LIF/LD  $\times$  100; the vertical line is the mean of the sample, and the horizontal line corresponds to  $\pm 2$  standard errors of the mean.

a form that lacks any anterior projection of the zygomatic plate.

**DENTITION**—The molar topography characteristic of *Voalavo* and *Eliurus* offers several points of similarity suggestive of their near kin-

ship. Compared with the brachyodont teeth of *Macrotarsomys* and *Monticolomys*, their molars are moderately hypsodont, the higher crowns achieved both through vertical elongation of the laminae and the molar bases. The occlusal sur-

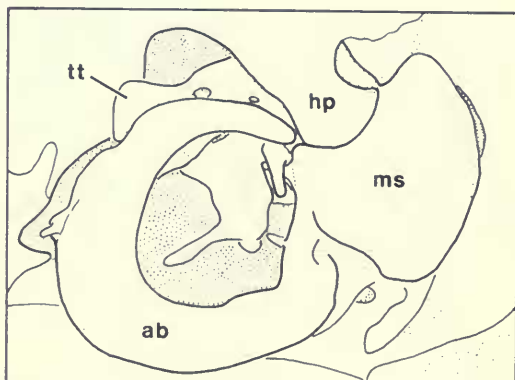
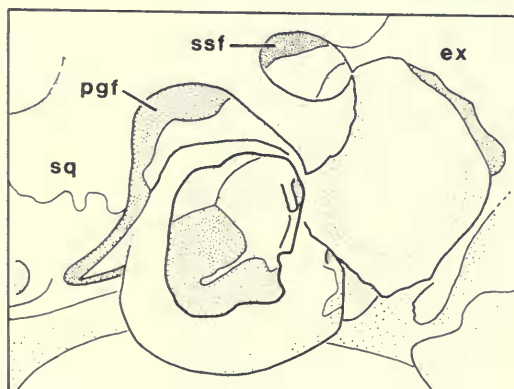


FIG. 11-15. Left lateral view of the otic region and associated foramina. **Left**, *Voalavo gymnocaudus* (FMNH 156162; Antsiranana Province, RS d'Anjanaharibe-Sud). **Right**, *Eliurus minor* (USNM 449246; Fianarantsoa Province, 3 km NNW of Vohiparara). ab = auditory bulla (ectotympanic); ex = exoccipital; hp = hamular process; ms = mastoid capsule of periotic; pgf = postglenoid foramen; sq = squamosal; ssf = subsquamosal fenestra; and tt = tegmen tympani. The tegmen tympani in members of *Eliurus* strongly abuts the squamosal bone, a connection not observed in *Voalavo*.

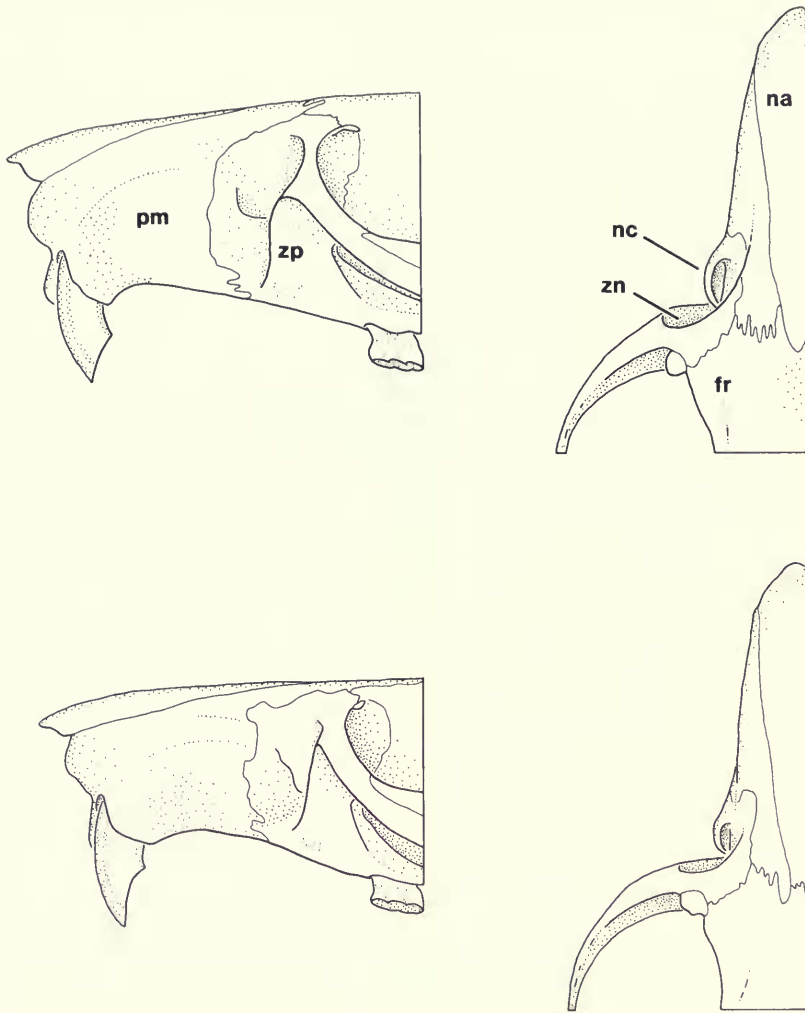


FIG. 11-16. Left lateral and dorsal views of the rostrum and anterior zygomatic region. **Top**, *Eliurus minor* (USNM 449246: Fianarantsoa Province, 3 km NNW of Vohiparara). **Bottom**, *Voalavo gymnocaudus* (FMNH 154041: Antsiranana Province, RS d'Anjanaharibe-Sud). fr = frontal; nlc = nasolacrimal capsule; na = nasal; pm = premaxilla; zn = zygomatic notch; and zp = zygomatic plate. Note the narrower zygomatic plate and indistinct notch in *Voalavo*.

faces are flat and configured as a series of nearly transverse laminae that lack anterior–posterior enamel connections (one exception in *Voalavo*, see below), except at their outer edges with advanced wear. The molar hypsodonty and lamination observed in *Eliurus* and *Voalavo* obscure discernment of cusp homology in formation of the laminae. Notwithstanding precise identification of homologous cusps, the arrangement of the laminae on the first and second molars, both upper and lower, is remarkably alike in the two genera (Fig. 11-17). The resemblance involves both the number of laminae on the anterior molars and the location of enamel folds or islands

on the lower first (metaflexid?) and upper second molars (postero flexus?). Three roots appear to anchor the upper molars and two anchor the lower molars in both genera.

Aside from their planar surfaces and transverse orientation of enamel structures, the molar dentitions of *Eliurus* and *Voalavo* reveal several prominent differences. The upper and lower third molars of *Voalavo* are noticeably smaller than their anterior counterparts, about one-half the size of the contiguous second molars whether compared in terms of length or area (Fig. 11-17). Among species of *Eliurus*, the third molars either approximately match the second ones (*E.*

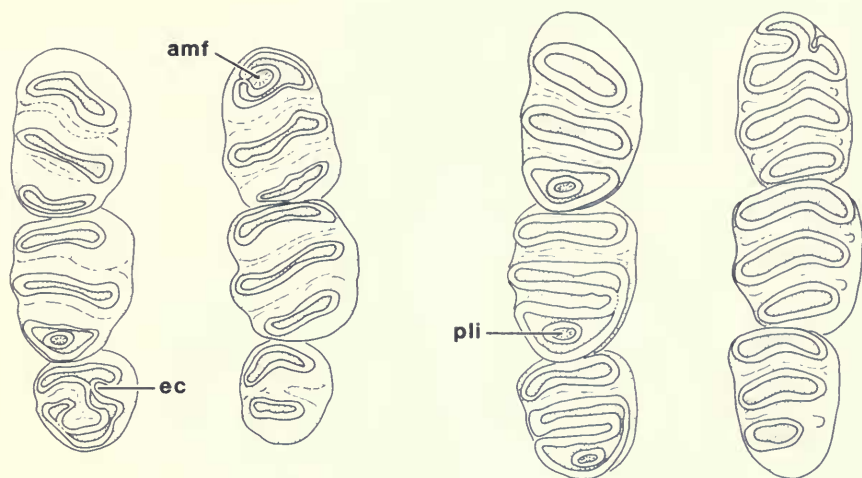


FIG. 11-17. Occlusal views of the upper (left member) and lower (right member) right molar rows. **Left pair**, *Voalavo gymnocaudus* (FMNH 156162; Antsiranana Province, RS d'Anjanaharibe-Sud). **Right pair**, *Eliurus minor* (USNM 449247; Fianarantsoa Province, 3 km NNW of Vohiparara). amf = anteromedial enamel fold (metaflexid?) of M1; ec = enamel connection (median mure?) of M3; and pli = posterolateral enamel island (posterofofsetus?) of M2. Note the smaller third molars in the example of *Voalavo* and the occurrence of only two laminae on its lower third molar in contrast to three in all species of *Eliurus*.

*majori* and *E. penicillatus*) or attain about two-thirds their size (other species). In *Voalavo*, the lower third molar, perhaps in correlation with its smaller size, bears only two laminae, in contrast to the three uniformly defined on lower third molars of *Eliurus*. Lamination is not at all developed on the upper third molar of *Voalavo*. The small, circular M3 does have a transverse member across its front, perhaps homologous to the first lamina found in *Eliurus*, but the enamel surface of the rear is irregularly formed in the four specimens, usually with interconnected "cusps" surrounding a medial basin. A longitudinal enamel ridge, its position suggestive of a median mure, joins the anterior and posterior sections of M3 in *Voalavo*, whereas such a medial connection is rarely found in *Eliurus*, the first and second laminae being completely segregated by a deep cleft across the width of the tooth. All species of *Eliurus* possess a posterolabial enamel fold (posterofofsetus?) at the posterior margin of each upper molar; with slight wear, the fold becomes isolated as an enamel island (posterofofsetus?), and with moderate to advanced wear, it becomes entirely obliterated. Only the second upper molar of *Voalavo* exhibits such a fold (Fig. 11-17). Although we characterize the crowns of both *Voalavo* and *Eliurus* as moderately hypsodont, those of the latter genus appear uniformly higher. The descriptive

terminology so far advanced for muroid molar specialization is insufficient to meaningfully discriminate such subtle and graded differences in hypsodonty.

### Phylogenetic Relationships

The generic attributes of the seven long-established genera of Nesomyinae—*Hypogeomys* A. Grandidier (1869), *Nesomys* Peters (1870), *Brachytarsomys* Günther (1875), *Eliurus* Milne Edwards (1885), *Brachyuromys* Major (1896b), *Gymnuromys* Major (1896b), and *Macrotarsomys* Milne Edwards and G. Grandidier (1898)—are so sharply marked that hierarchical patterns of kinship among them are obscure. Ellerman's (1941) dissolution of the group indirectly admits this point, although the validity of his reclassification would profit from actual analysis of characters and phylogenetic reconstruction to be sure. However, like the recently diagnosed *Monticolomys* (Carleton & Goodman, 1996), the elfin nesomyine from RS d'Anjanaharibe-Sud represents another instance of a new genus with demonstrable phyletic affiliation with a previously described form, in this case *Eliurus*. In fact, definition of *Voalavo* and *Eliurus* each rests upon their own collection of synapomorphic traits and suggests that the

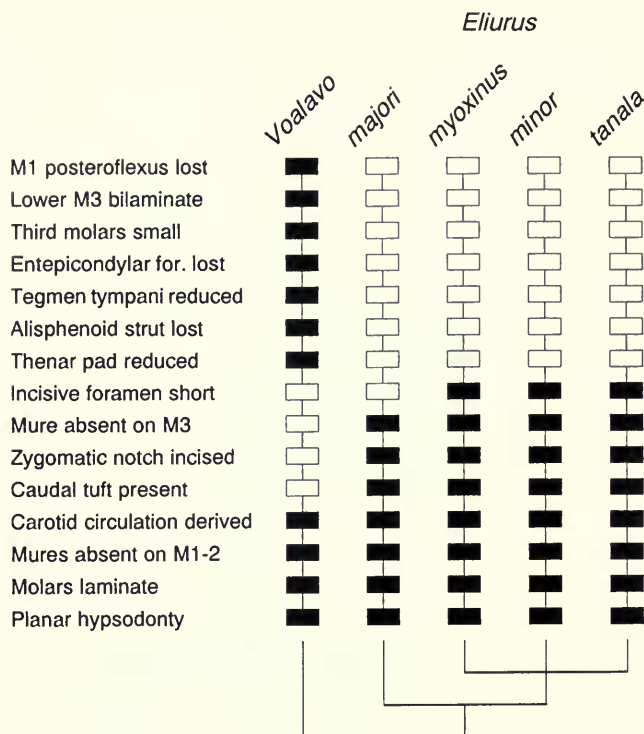


FIG. 11-18. Distribution of presumptive synapomorphies (solid rectangles) and hypothesized cladistic relationship between *Voalavo gymnocaudus*, new genus and species, and representative species of *Eliurus* Milne Edwards (1885). The latter include the type species (*E. myoxinus*), the smallest (*E. minor*) and largest (*E. tanala*) forms within the genus, and a highly differentiated, perhaps cladistically primitive species (*E. majori*).

small eliurine without a caudal tuft is not merely a derivative species of the latter (Fig. 11-18).

*Voalavo* and *Eliurus* possess several synapomorphic character states that support their near kinship exclusive of other nesomyines. Perhaps the most persuasive among these are certain dental features, such as the nature of their molar hypsodonty, attainment of a planar occlusal surface, and development of lamination. The laminate architecture of their teeth appears to involve the same transverse connections of cusps and attendant loss of accessory crests (mures-ids, mesolophs-ids?), at least for the first and second molars. Evolutionary rearrangement of distal branches of the stapedia artery, mirrored in the loss of certain foramina (stapedial and sphenofrontal) and vascular imprints (squamosal-alisphenoid and parapterygoid grooves), characterizes the skulls of *Voalavo* and *Eliurus*; however, a derived carotid circulation is also common to *Brachytarsomys*, *Brachyuromys*, *Gymnuromys*, and *Hypogeomys*. Other details of morphological agreement between the two—hindfoot conformation, ungual

tufts, interorbital shape, lack of supraorbital shelf and temporal ridging, dorsal extension of the alisphenoid, unremarkable construction of the auditory bullae, and thoracolumbar formula—may be reasonably attributed to symplesiomorphic resemblance. The comparatively elongate incisive foramen typical of *Voalavo* and some *Eliurus* (*E. majori* and *E. penicillatus*) is here interpreted as a primitive condition; polarity for this character, however, is ambiguous when muroids are broadly considered (see Carleton, 1994, for references on divergent viewpoints).

In spite of their morphological similarities, and wanting a full phylogenetic review of the Nesomyinae, generic separation of *Voalavo* and *Eliurus* is defensible on the basis of the association of certain discrete characteristics unique to each. Individuals of *Voalavo* possess several autapomorphies (autapomorphic within our narrow systematic context), involving characters of the foot, cranium, humerus, and molar dentition, that set them apart from *Eliurus* (Fig. 11-18). Generic recognition for the new species *gymnocaudus* does



not leave the diagnosis of *Eliurus* as a paraphyletic construct. The monophyly of that genus is supported by other apomorphies, among them possession of an elaborately penicillate tail, formation of a broader zygomatic plate and distinct notch, and suppression of a mure on the upper third molar. That *Voalavo* retains the plesiomorphic state for each of these three characters suggests that it diverged from a common ancestor before the radiation of tufted-tailed rats, the most speciose of the nesomyine genera.

## Biogeography

The inventory of RS d'Anjanaharibe-Sud is the first detailed survey of the rodent fauna of the northern highlands of Madagascar. Earlier work in this region involved only cursory trapping of small mammals and often failed to preserve voucher specimens (e.g., Albignac, 1970; Duckworth & Rakotondrapary, 1990). The discovery of three species of small mammals new to science (see also Chapter 10) based on material obtained in the RS d'Anjanaharibe-Sud underscores how little was known about the fauna of this region.

Elevational transects conducted over the past few years, as well as synthesis of material collected earlier, have provided clearer information on the altitudinal zonation of nesomyine rodents in the eastern humid forest (Carleton & Schmidt, 1990; Carleton, 1994; Goodman & Carleton, 1996; Goodman et al., 1996; Langrand & Goodman, 1997; Chapter 12). In general, most species have well-circumscribed elevational limits that are apparently related to factors associated with vegetational communities. These limits appear to be constant across the latitudinal range of rodent species. The five specimens of *Voalavo gymnocaudus* reported here were taken in two different vegetational zones on the Anjanaharibe-Sud Massif, sclerophyllous forest near the summit at 1950 m and moist montane forest on the western slope at 1300 m.

Judged by paleoecological data from pollen cores taken at several sites on Madagascar (Straka, 1996; Burney, 1997), the distinctive, modern high-mountain vegetational communities descended to approximately 1000 m during certain Quaternary periods when the climate was cooler and drier. Ridges of 1000 m and higher between highland areas would have formed bridges of high-mountain vegetation and provided dispersal corridors for organisms such as *Voalavo*

*gymnocaudus*. On the basis of such a model, this species should be found to occur broadly across the northern highlands (Fig. 11-19), in regions such as the RNI de Marojejy, the upper zone of the Tsaratanana Massif (2876 m), and satellite peaks to the east and southeast, such as Andramanalana (2260 m) and Biempoko (2219 m). *Voalavo* doubtfully occurs on the Manongarivo Massif, which is separated from these northern highlands by a zone less than 1000 m, or on the isolated Montagne d'Ambre to the far north. The Tsaratanana Massif remains one of most poorly known mountainous areas of Madagascar. Continued zoological exploration of this region will verify whether the proposed model of vegetational shifts can explain the distribution of the high mountain fauna.

## Coda

The native rodents of Madagascar have been traditionally characterized as an insular radiation of inordinately low species diversity, an anomaly remarked upon by biogeographers and systematists (Darlington, 1957; Paulian, 1984; Woods & Eisenberg, 1989). The meager diversity of Nesomyinae seemed at odds with Madagascar's size, topographic relief, climatic and floristic complexity, and the ecogeographic opportunities for speciation and phyletic differentiation presumably offered. Certainly, a total of only 10 species, as nesomyine alpha taxonomy was misunderstood for much of the 20th century (following Ellerman, 1949; Petter, 1972, 1975), is conspicuously depauperate compared with rodent assemblages that have populated other large islands occurring within tropical latitudes (Fig. 11-20).

The picture of exceptional impoverishment changed abruptly in the 1990s, a reassessment catalyzed by basic revisionary study and field inventory (Carleton & Schmidt, 1990; Carleton, 1994; Carleton & Goodman, 1996; Goodman & Carleton, 1996; this chapter; Chapter 12). The number of nesomyine species recognized as valid has accordingly doubled in this short interval, elevating the diversity of the subfamily closer to that predicted on the basis of island area (Fig. 11-20). Although recent work has revised upwardly the number of Nesomyinae, the expectation that their specific diversity will match that of rodents on comparably sized tropical islands seems doubtful, even admitting the new forms that will be discov-

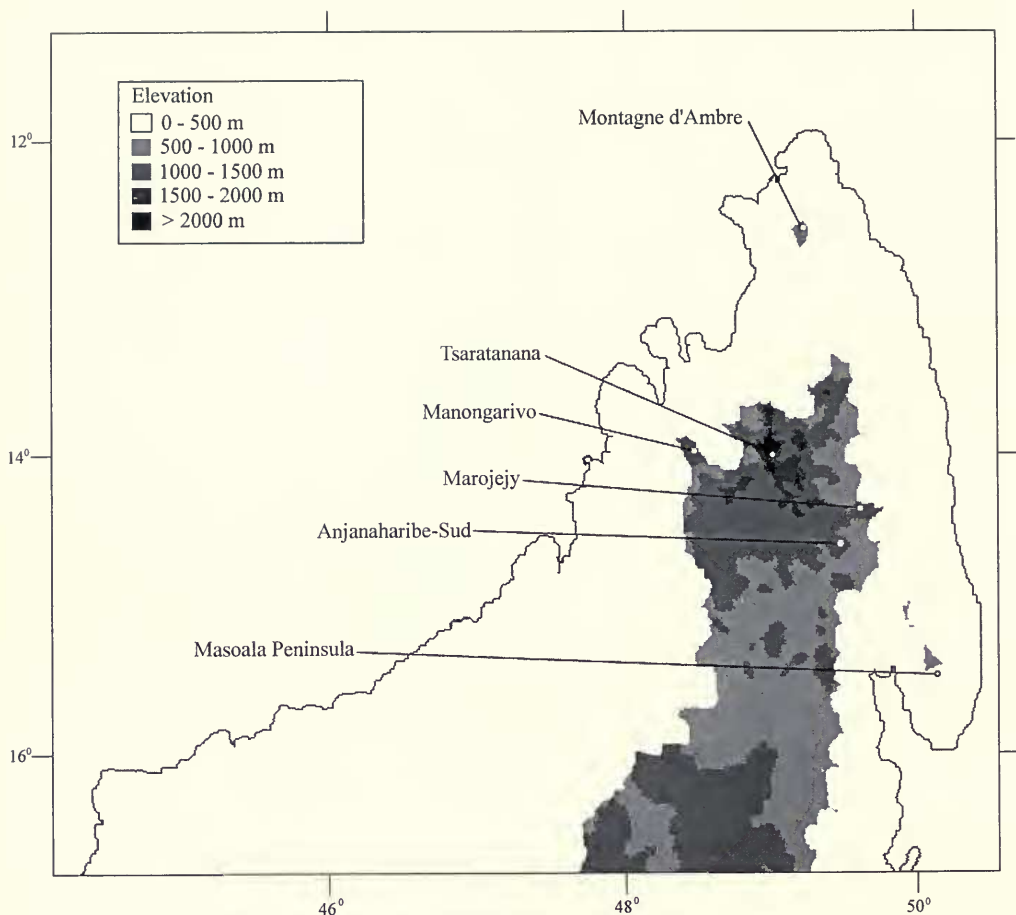


FIG. 11-19. Topographic map of northern Madagascar showing elevational connections between different massifs of the northern highlands.

ered or resurrected from synonymy in the next 5 years. Islands slightly larger than Madagascar, like Borneo and New Guinea, support rodent faunas of 55–60 species (Medway, 1977; Musser, 1987; Flannery, 1995); even islands slightly smaller, like Sulawesi and Sumatra, contain 40–46 species (Heaney, 1986; Musser, 1987). Either range of figures appears unrealistic for Madagascar, based on what has been documented to date and considering what areas have yet to be explored and which genera have yet to be revised.

We anticipate that the trajectory of future research on Madagascar's indigenous species will divulge around 30–35 species. Although not as depauperate as once supposed, considerable difference still exists between this firmer estimate (30–35 species) of Malagasy rodents and that based on the species-area curve derived for other Old World tropical islands (50–55 species). The

disparity invites other explanations beyond the mostly correctable artifacts of antiquated taxonomy and insufficient field survey.

Foremost among the biological alternatives is the notion that ecological niches typically filled by rodents were already occupied by an earlier Tertiary radiation of lemurs and tenrecs before the arrival of nesomyines, e.g., as noted by Woods and Eisenberg (1989). The unbalanced faunal composition of nesomyine rodents and strepsirrhine primates (32 extant species, *sensu* Mittermeier et al., 1994) attracts immediate attention in comparison with the usual predominance of rodents relative to primate species on other paleotropical islands (4 to 10 times as many; see Carleton & Schmidt, 1990: Table 2). Moreover, several of the Malagasy lemurs, such as *Cheirogaleus* and *Microcebus*, are relatively small-bodied and arboreal, resembling, e.g., the nesomyine *Brachy-*

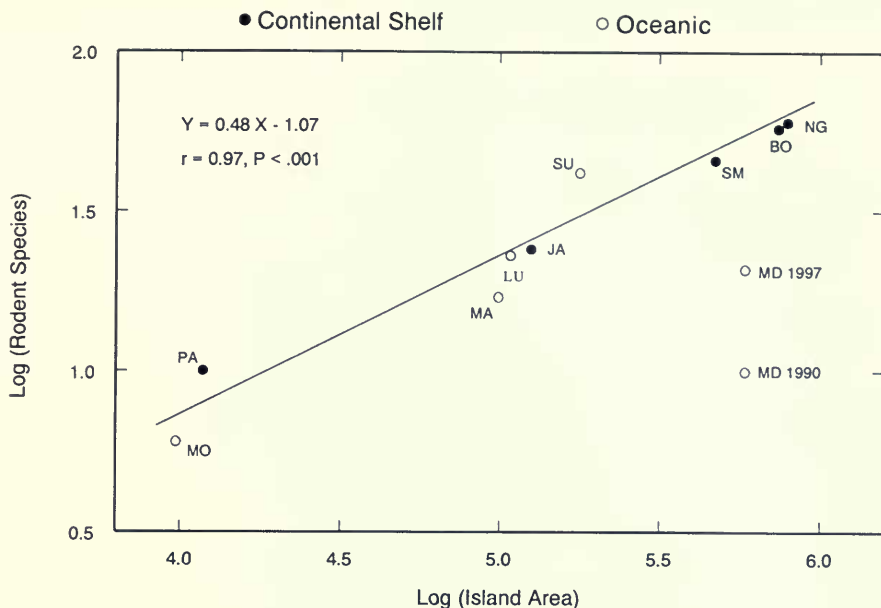


FIG. 11-20. Relationship between log of island area and log of number of indigenous rodent species for large islands with diverse tropical floras. Madagascar was not included in the calculation of the regression statistics ( $N = 9$ ); see Carleton and Schmidt (1990: Table 2) for island areas, number of rodent species, and literature sources. The intervening years (1990–1997) of taxonomic revision and field exploration have increased the number of indigenous rodent species on Madagascar closer to that predicted on the basis of the island's area (see text for discussion). BO = Borneo; JA = Java; LU = Luzon; MA = Mindinao; MD = Madagascar; MO = Mindoro; NG = New Guinea; PA = Palawan; SM = Sumatra; and SU = Sulawesi.

*tarsomys* in habits and somewhat in size (see Chapter 12).

Renewed appreciation of the biodiversity of tenrecid insectivores is still emerging, particularly for *Microgale*, with new descriptions and revisions rapidly overturning MacPhee's (1987) improbably low estimate of just 10 species (Jenkins, 1988, 1992, 1993; Jenkins et al., 1996, 1997; Chapter 10). A conspicuous trophic absence among the Nesomyinae, in light of the morphological variety and ecological specializations exhibited by the oryzorictine tenrecs, is the guild of long-snouted, short or long-tailed, small or large-bodied shrew rats and mice. The radiation of murids into such insectivorous and vermivorous niches is commonplace on other tropical islands and archipelagos, such as New Guinea, the Philippines, and Sulawesi (Musser & Freeman, 1981; Musser, 1982, 1987; Flannery, 1995). As currently known, no nesomyine displays such specialized cranial and dental morphologies and the trophic habits they presuppose. Except for the brachyodont, cuspidate molars of *Macrotarsomys* and *Monticolomys*, other nesomyines possess moderate to well-developed hypsodonty (none is hyp-

selodont), and many have prismatic or planar occlusal surfaces with suppression of individual cusps, features that suggest reliance on a herbivorous diet or some mix of granivory and herbivory. With the hydrological sculpting along Madagascar's rugged eastern escarpment, the opportunity for evolution of semiaquatic insectivorous rodents, like those found on New Guinea (Flannery, 1995) and in the Neotropics (Voss, 1988), would seem possible if not likely. Here again, such a semiaquatic habitus on Madagascar was not exploited by nesomyines but is filled by the water tenrec *Limnogale mergulus*.

The applicability of a niche saturation hypothesis, in some form, is worthy of rigorous exploration and firmer argument with regard to the Nesomyinae. Between them, the lemuriform primates and tenrecid insectivores of Madagascar appear to have preempted many ecological niches otherwise filled by rodents in other isolated settings, whether continental (Australia and South America) or insular (New Guinea and Sulawesi) in scale. Another hypothesis, the occurrence of dramatic recent extinctions, associated either with climatic shifts, habitat degradation, or the possible



introduction of hyperdiseases (Burney, 1987; MacPhee & Marx, 1997), remains as intriguing a question for Madagascar's rodents as for its lemurs. A requisite corollary to acceptance of any such explanation, or their combination, is further research on the number and kinds of nesomyine species, their distributions, and their natural histories. The continuing need for investigation of these fundamental sorts hardly bears repetition, nor does restatement of their urgency against the pressures of burgeoning human populations and ever-dwindling natural environments within a fragile insular setting.

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### Literature Cited

ALBIGNAC, R. 1970. Mammifères et oiseaux du Massif du Tsaratanana. Mémoires ORSTOM, **37**: 223–229.  
ARCHBOLD, R. 1930. Bevato, a camp in Madagascar. Natural History, **30**: 645–652.  
BUGGE, J. 1970. The contribution of the stapedia artery to the cephalic arterial supply in muroid rodents. Acta Anatomica, **76**: 313–336.

BURNEY, D. A. 1987. Pre-settlement vegetation changes at Lake Tritrivakely, Madagascar. Paleogeography of Africa, **18**: 357–381.  
———. 1997. Theories and facts regarding Holocene environmental change on Madagascar before and after human colonization, pp. 75–89. In Goodman, S. M., and B. D. Patterson, eds., Natural Change and Human Impact in Madagascar. Smithsonian Institution Press, Washington, D.C. xiii + 432 pp.  
CARLETON, M. D. 1980. Phylogenetic relationships in neotomine–peromyscine rodents (Muroidea) and a reappraisal of the dichotomy within New World Cricetinae. Miscellaneous Publications of the Museum of Zoology, University of Michigan, **157**: 1–146.  
———. 1994. Systematic studies of Madagascar's endemic rodents (Muroidea: Nesomyinae): Revision of the genus *Eliurus*. American Museum Novitates, **3087**: 1–55.  
CARLETON, M. D., AND S. M. GOODMAN. 1996. Systematic studies of Madagascar's endemic rodents (Muroidea: Nesomyinae): A new genus and species from the Central Highlands, pp. 231–256. In Goodman, S. M., ed., A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation. Fieldiana: Zoology, n.s., **85**: 1–319.  
CARLETON, M. D., AND G. G. MUSSER. 1984. Muroid rodents, pp. 289–379. In Anderson, S., and J. K. Jones, Jr., eds., Orders and Families of Recent Mammals of the World. John Wiley and Sons, New York, 686 pp.  
———. 1989. Systematic studies of oryzomyine rodents (Muridae, Sigmodontinae): A synopsis of *Microoryzomys*. Bulletin of the American Museum of Natural History, **191**: 1–83.  
CARLETON, M. D., AND D. F. SCHMIDT. 1990. Systematic studies of Madagascar's endemic rodents (Muroidea: Nesomyinae): An annotated gazetteer of collecting localities of known forms. American Museum Novitates, **2987**: 1–36.  
DARLINGTON, P. J. 1957. Zoogeography: The Geographical Distribution of Animals. Wiley Press, New York, xi + 675 pp.  
DUCKWORTH, J. W., AND F. RAKOTONDRAPARANY. 1990. The mammals of Marojeje, pp. 54–60. In Safford, R., and Duckworth, J. W., eds., A Wildlife Survey of the Marojeje Nature Reserve, Madagascar. International Council for Bird Preservation, Cambridge.  
ELLERMAN, J. R. 1941. The Families and Genera of Living Rodents. Volume 2, Family Muridae. British Museum (Natural History), London, xii + 690 pp.  
———. 1949. The Families and Genera of Living Rodents, volume 3, appendix II [notes on the rodents from Madagascar in the British Museum, and on a collection from the island obtained by Mr. C. S. Webb]. British Museum (Natural History), London, v + 210 pp.  
FLANNERY, T. 1995. Mammals of New Guinea. Cornell University Press, Ithaca, N.Y. 568 pp.  
GOODMAN, S. M. 1995. The third known specimen of the Red-tailed Newtonia *Newtonia fanovanae* (Family Sylviidae), a Malagasy endemic. Bulletin of the British Ornithologists' Club, **115**: 130–132.



- GOODMAN, S. M., A. ANDRIANARIMISA, L. E. OLSON, AND V. SOARIMALALA. 1996. Patterns of elevational distribution of birds and small mammals in the humid forest of Montagne d'Ambre, Madagascar. *Ecotropica*, **2**: 87–98.
- GOODMAN, S. M., AND M. D. CARLETON. 1996. The rodents of the Réserve Naturelle Intégrale d'Andringitra, Madagascar, pp. 257–283. In Goodman, S. M., ed., A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation. *Fieldiana: Zoology*, n.s., **85**: 1–319.
- GRANDIDIER, A. 1869. Description de quelques animaux nouveaux découverts, pendant l'année 1869, sur la côte ouest de Madagascar. *Revue et Magazin de Zoologie*, Paris, série 2, **21**: 337–342.
- GÜNTHER, A. 1875. Notes on some mammals from Madagascar. *Proceedings of the Zoological Society of London*, **1875**: 78–80.
- HEANEY, L. R. 1986. Biogeography of the mammals of SE Asia: Estimates of rates of colonization, extinction, and speciation. *Biological Journal of the Linnean Society*, **28**: 127–165.
- HERSHKOVITZ, P. 1962. Evolution of Neotropical cricetine rodents (Muridae) with special reference to the phyllotine group. *Fieldiana, Zoology*, **46**: 1–524.
- JENKINS, P. D. 1988. A new species of *Microgale* (Insectivora: Tenrecidae) from northeastern Madagascar. *American Museum Novitates*, **2910**: 1–7.
- . 1992. Description of a new species of *Microgale* (Insectivora: Tenrecidae) from eastern Madagascar. *Bulletin of the British Museum Natural History (Zoology)*, **58**: 53–59.
- . 1993. A new species of *Microgale* (Insectivora: Tenrecidae) from Eastern Madagascar, with an unusual dentition. *American Museum Novitates*, **3067**: 1–11.
- JENKINS, P. D., S. M. GOODMAN, AND C. J. RAXWORTHY. 1996. The shrew tenrecs (*Microgale*) (Insectivora: Tenrecidae) of the Réserve Naturelle Intégrale d'Andringitra, Madagascar, pp. 191–217. In Goodman, S. M., ed., A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation. *Fieldiana: Zoology*, n.s., **85**: 1–319.
- JENKINS, P. D., C. J. RAXWORTHY, AND R. A. NUSSBAUM. 1997. The description of a new species of *Microgale* (Insectivora, Tenrecidae), with comments on the status of four related taxa. *Bulletin of the British Museum Natural History (Zoology)*, **63**: 1–12.
- LANGRAND, O., AND S. M. GOODMAN. 1997. Inventaire des oiseaux et des micro-mammifères des zones sommitales de la Réserve Naturelle Intégrale d'Andringitra. *Akon'ny Ala*, **20**: 39–54.
- LANGRAND, O., AND SINCLAIR. 1994. Additions and supplements to the Madagascar avifauna. *Ostrich*, **65**: 302–310.
- MACPHEE, R. D. E. 1987. The shrew tenrecs of Madagascar: Systematic revision and Holocene distribution of *Microgale* (Tenrecidae, Insectivora). *American Museum Novitates*, **2889**: 1–45.
- MACPHEE, R. D. E., AND P. A. MARX. 1997. The 40,000 plague: Humans, hyperdisease, and first-contact extinctions, pp. 169–217. In Goodman, S. M., and B. D. Patterson, eds., *Natural Change and Human Impact in Madagascar*. Smithsonian Institution Press, Washington, D.C.
- MAJOR, C. I. FORSYTH. 1896a. Descriptions of four additional new mammals from Madagascar. *Annals and Magazine of Natural History*, series 6, **18**: 461–463.
- . 1896b. Diagnoses of new mammals from Madagascar. *Annals and Magazine of Natural History*, series 6, **18**: 318–325.
- MEDWAY, L. 1977. The Mammals of Borneo, 2nd edition. *Monograph of the Malayan Branch of the Royal Asiatic Society*, **7**: 1–172.
- MILNE EDWARDS, A. 1885. Description d'une nouvelle espèce de rongeur provenant de Madagascar. *Annales des Sciences naturelles, Zoologie et Paléontologie (Paris)*, **20**: Article 1 bis.
- MILNE EDWARDS, A., AND G. GRANDIDIER. 1898. Description d'une espèce nouvelle de Muride provenant de Madagascar. *Bulletin du Muséum National d'Histoire Naturelle*, série 1, **4**: 179–181.
- MITTERMEIER, R. A., I. TATTERSALL, W. R. KONSTANT, D. M. MEYERS, AND R. B. MAST. 1994. *Lemurs of Madagascar*. Conservation International, Washington D.C., 356 pp.
- MUSSER, G. G. 1982. Results of the Archbold expeditions. No. 110. *Crunomys* and the small-bodied shrew rats native to the Philippine Islands and Sulawesi (Celebes). *Bulletin of the American Museum of Natural History*, **174**: 1–95.
- . 1987. The mammals of Sulawesi, pp. 73–93. In Whitmore, T. C., ed., *Biogeographic Evolution of the Malay Archipelago*. Clarendon Press, Oxford, x + 147 pp.
- MUSSER, G. G., AND M. D. CARLETON. 1993. Family Muridae, pp. 501–755. In Wilson, D. E., and D. M. Reeder, eds., *Mammal Species of the World: A Taxonomic and Geographic Reference*, 2nd ed. Smithsonian Institution Press, Washington, D.C., xviii + 1207 pp.
- MUSSER, G. G., AND P. W. FREEMAN. 1981. A new species of *Rhynchomys* (Muridae) from the Philippines. *Journal of Mammalogy*, **62**: 154–159.
- PAULIAN, R. 1984. Introduction to the mammals, pp. 151–154. In Jolly, A., P. Oberlé, and R. Albignac, eds., *Key Environments: Madagascar*. Pergamon Press, Oxford, xviii + 239 pp.
- PETERS, W. 1870. Über *Nesomys rufus*, eine neue gattung und art madagascarischer nager. *Sitzungs-Berichte der Gesellschaft naturforschender Freunde*, Berlin, **1870**: 54–55.
- PETTER, F. 1972. The rodents of Madagascar: The seven genera of Malagasy rodents, pp. 661–665. In Battistini, R., and G. Richard-Vindard, eds., *Biogeography and Ecology in Madagascar*. W. Junk, The Hague, xv + 765 pp.
- . 1975. Family Cricetidae: Subfamily Nesomyinae. Part 6.2, pp. 1–4. In Meester, J., and H. W. Setzer, eds., *The Mammals of Africa: An Identification Manual*. Smithsonian Institution Press, Washington, D.C.
- REIG, O. A. 1977. A proposed unified nomenclature for the enamelled components of the molar teeth of the

- Cricetidae (Rodentia). Journal of Zoology, London, **181**: 227–241.
- STRAKA, H. 1996. Histoire de la végétation de Madagascar oriental dans les derniers 100 millénaires, pp. 37–47. In Lourenço, W. R., ed., Biogéographie de Madagascar. ORSTOM Editions, Paris.
- THOMAS, O. 1895. On a new species of *Eliurus*. Annals and Magazine of Natural History, series 6, **16**: 164–165.
- VIETTE, P. 1991. Principales localités où des Insectes ont été recueillis à Madagascar. Faune de Madagascar, supplément 2. Private printing.
- VOSS, R. S. 1988. Systematics and ecology of ichthyomyine rodents (Muroidea): Patterns of morphological evolution in a small adaptive radiation. Bulletin of the American Museum of Natural History, **188**: 259–493.
- . 1993. A revision of the Brazilian muroid rodent genus *Delomys* with remarks on “thomasoniine” characters. American Museum Novitates, **3073**: 1–44.
- VOSS, R. S., AND M. D. CARLETON. 1993. A new genus for *Hesperomys molitor* Winge and *Holochilus magnus* Hershkovitz (Mammalia, Muridae) with an analysis of its phylogenetic relationships. American Museum Novitates, **3085**: 1–39.
- WOODS, C. A., AND J. F. EISENBERG. 1989. The land mammals of Madagascar and the Greater Antilles: Comparison and analysis, pp. 799–826. In Woods, C. A. ed., Biogeography of the West Indies: Past, Present, and Future. Sandhill Crane Press, Gainesville, Fla., xviii + 878 pp.

## Appendix 11-1.

### Comparative Material

Listed below are specimens of *Eliurus* from outside the RS d'Anjanaharibe-Sud that formed the basis for the sample statistics, tabular comparisons, and morphometric analyses presented in the various species accounts. They are contained in the following museums: British Museum (Natural History) (BMNH), London; Field Museum of Natural History (FMNH), Chicago; Merseyside County Museums, Liverpool (LMCM); Museum of Comparative Zoology (MCZ), Harvard University, Cambridge; Muséum National d'Histoire Naturelle (MNHN), Paris; National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.; and Universitets Zoologisk Museum, Copenhagen (UZMC).

*Eliurus ellermani*—Toamasina Province: Hiarakaka, near Maroantsetra, 850 m (MNHN 1981.871, holotype); 13 mi N of Rogez, near Lohariandava, 1300 ft (BMNH 47.1623).

*Eliurus minor*—Fianarantsoa Province: Ambodiamontana, 7 km W of Ranomafana, 950 m (USNM 448974–448980, 448998); 14 km E of Andraina (USNM 328826); 3 km (by road) NNW of Vohiparara, 1225 m (USNM 449246–449249).

*Eliurus myoxinus*—Toliara Province: Analabe, 60 km N of Morondava (MNHN 1980.290, 1982.988); Beroboka, 40 mi N of Morondava (BMNH 47.1608, 47.1609, 1987.50); 5 mi E of Bevilany, Ambovombe–Fort Dauphin road, 800 ft (BMNH 47.1600–47.1607, 66.2746); Morondava (MNHN 1973.516); Tsilambana (MNHN 1886.1120, holotype); 35 mi E of Tulear (BMNH 47.1610, 47.1611, 47.1611a).

*Eliurus penicillatus*—Fianarantsoa Province: Ampitambe (BMNH 97.9.1.148–97.9.1.150, 97.9.1.152, 1939.1892; FMNH 5630, 18822; LMCM A19.4.98.26; MCZ 12435, 45932; MNHN 1897.536, 1909.191; USNM 49672; UZMC 1219, 1224, 7941).

*Eliurus petteri*—Toamasina Province: 8 km from Fanovana (MNHN 1961.177, holotype); 18 km E of Périnet (USNM 341825); north of Rogez (MCZ 45928).

*Eliurus tanala*—Fianarantsoa Province: Ambodiamontana, 7 km (by road) W of Ranomafana, 950 m (USNM 448981–448990, 449250–449256); 1 km NW of Andrambovato, 875 m (USNM 449256); RNI d'Andringitra, 38–43 km S of Ambalavao, 810–1625 m (FMNH 151687–151692, 151743, 151744, 151869, 151870, 151873, 151874, 151880, 151881); Vinanitelo, 30 mi S of Fianarantsoa (BMNH 97.9.1.154, holotype; FMNH 5631; MCZ 45690); 3 km (by road) NNW of Vohiparara, 1225 m (USNM 449251–449255). Toamasina Province: 10 mi NW of Lohariandava, 1500 ft (BMNH 47.1573); Périnet, near Moramanga, 3000 ft (BMNH 47.1557, 47.1560–47.1568, 47.1571, 47.1572; MNHN 1961.176); 1 km E of Périnet (USNM 341826); 2 km E of Périnet (USNM 328828, 328829); 13 km E of Périnet (USNM 341827). Toliara Province: RNI d'Andohahela (FMNH 156515, 156519–156521, 156531, 156532, 156628, 156631, 156634–156641).

*Eliurus webbi*—Fianarantsoa Province: 2 km NE of Andrambovato, 575 and 625 m (USNM 449266–449268); 1 km NW of Andrambovato, 875 m (USNM 449269); 12 km E of Ifanadiana (MNHN 1961.216–1961.219); 0.5 km N of Kianjavato, 300 m (USNM 448991–448995); 9 km ESE of Kianjavato, 250–500 m (USNM 449257–449265).